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Wildlife Research Report 13

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HERPETOLOGICAL COMMUNITIES

A Symposium of the Society for the Study of Amphibians and Reptiles and the Herpetologists' League, August 1977

Edited by
Norman J. Scott, Jr.

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I

Dedicated to the Memory
of
Howard W. "Duke" Campbell, Wildlife Biologist,
Denver Wildlife Research Center, Gainesville, Florida.

Preface

The idea that organisms occur in communities of species whose interactions produce distinct community characteristics is relatively new. Before 1960, most ecological investigations of reptiles and amphibians were aimed at the production of autecological studies of single species or simple lists of species present. Since then, the study of communities or community segments has become more popular, but work of this type still accounts for only a small part of the herpetological literature. The present volume originated as a symposium at the Lawrence, Kansas, meetings of the Herpetologists' League and the Society for the Study of Amphibians and Reptiles on 9-10 August 1977. The purpose of the symposium was to provide a vehicle whereby reviews and original research articles dealing with herpetological communities could be incorporated into a single source. The diversity of ideas, study systems, techniques, and approaches will, I hope, stimulate workers to look at their own herpetological paradigm with an eye towards more integrative analyses of community structure and function.

For the purposes of the symposium, a herpetological community was defined as three or more reptile or amphibian species interacting (or potentially interacting) in the same habitat. This definition allowed the inclusion of very simple communities, such as Mautz's cave lizards, but eliminated studies based on single species or on isolated, two-species interactions. The rationale for this definition is that specific community characteristics begin to appear as the higher order effects of several species interacting, whereas autecological or pair-wise studies can be (and often are) carried out without gaining much insight into community-level dynamics.

This volume is organized into subject matter sections. Two review papers are followed by eight studies of amphibian, snake, and lizard communities, four studies of entire assemblages from tropical and sandy soil habitats, and three papers dealing with field techniques for the study of herpetofaunal communities. The final paper gives a historical resumé of herpetological community studies, a summary of the papers included in the volume, and recommendations for the future. This paper is followed by a chronological bibliography of herpetofaunal community studies.

Many people helped in the preparation of this volume. Each contribution was reviewed several times and reviewers are acknowledged in the individual papers. I am especially grateful to R. E. Robino, Denver Wildlife Research Center, Albuquerque, who was instrumental in editing the manuscripts for final submission and who shared the entire process from beginning to end. I also thank Roy W. McDiarmid, Denver Wildlife Research Center, Washington, D.C., who read and commented on the entire manuscript and provided much needed support during the editing process. I thank the authors for their cooperation, both in revising their own papers and reviewing the contributions of others, and for their patience during the long lag between submission and publication. A few of the papers have been recently revised but many have not been brought up-to-date since 1977.

Norman J. Scott, Jr.

Contents

Page

Preface . . . iii

Reviews . . . v

A review of structuring in Herpetofaunal Assemblages, by Harold Heatwole . . . 1

Amphibian Reproductive Ecology on the Community Level, by Martha L. Crump . . . 21

Amphibian Communities . . . 37

Anuran Succession at Temporary Ponds in a Post Oak-Savanna Region of Texas, by John A. Wiest, Jr. . . . 39

Prey Patterns and Trophic Niche Overlap in Four Species of Caribbean Frogs, by Kirkland L. Jones . . . 49

Snake Communities . . . 57

Niche Dimensions and Resource Partitioning in a Great Basin Desert Snake Community, by William S. Brown and William S. Parker . . . 59

Resources of a Snake Community in Prairie-Woodland Habitat of Northeastern Kansas, by Henry S. Fitch . . . 83

Use of a Mammalian Resource by a Chihuahuan Snake Community, by Robert P. Reynolds and Norman J. Scott, Jr. . . . 99

Lizard Communities . . . 119

Temporal and Spatial Resource Partitioning in a Chihuahuan Desert Lizard Community, by F. Michael Creusere and Walter G. Whitford . . . 121

Use of Cave Resources by a Lizard Community, by William J. Mautz . . . 129

Structure and Composition of Mojave Desert Reptile Communities Determined with a Removal Method, by R. Bruce Bury . . . 135

Tropical Herpetofauna . . . 143

The Herpetofauna of Forest Litter Plots from Cameroon, Africa, by Norman J. Scott, Jr. . . . 145

Sandy Soil Herpetofaunas . . . 151

Herpetofaunal Survey of the Sinai Peninsula (1967–77), with Emphasis on the Saharan Sand Community, by Yehudah L. Werner . . . 153

The Herpetological Components of Florida Sandhill and Sand Pine Scrub Associations, by Howard W. Campbell and Steven P. Christman . . . 163

Food Resource Partitioning of Fossorial Florida Reptiles, by Charles R. Smith . . . 173

Techniques of Community Analysis . . . 179

Tracking as an Aid in Ecological Studies of Snakes, by Harvey B. Lillywhite . . . 181

Field Techniques for Herpetofaunal Community Analysis, by Howard W. Campbell and Steven P. Christman . . . 193

Evaluation of Techniques for Assessment of Amphibian and Reptile Populations in Wisconsin, by Richard C. Vogt and Ruth L. Hine . . . 201

Summary of Herpetological Community Studies . . . 219

A Chronological Bibliography, the History and Status of Studies of Herpetological Communities, and Suggestions for Future Research, by Norman J. Scott, Jr. and Howard W. Campbell . . . 221

REVIEWS

V

A Review of Structuring in Herpetofaunal Assemblages

by

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Abstract

The structuring of herpetofaunal assemblages in terms of numbers of species and individuals, equitability, biomass, spacing, and niche characteristics is reviewed, and the roles of moisture and altitude are evaluated. The contrast is made between forests and deserts as herpetological habitats, and some of the differences between the reptilian and amphibian components of assemblages are examined. The role of social organization in community structure, especially territoriality, is briefly mentioned.

A biotic community is an assemblage of organisms living together and interacting, and includes all such organisms, at all trophic levels. Consequently, a community is not limited to specific taxa, and a "herpetological community" by definition is not an ecologically meaningful entity. However, it is important to examine the structuring and interactions among community members of the same taxon, or of a few taxa. In the present paper I follow Heyer (1967) in referring to those segments of communities made up of reptiles, amphibians, or both as "herpetofaunal assemblages."

A biotic community (or a component assemblage) is without rank in the sense that one can treat, for example, the rain forest community, the forest floor community of the rain forest, or the community in decaying logs on the forest floor of the rain forest. In the present context the scale is determined by the few studies previously carried out.

I examined the structuring of herpetofaunal assemblages from several viewpoints: (1) numbers of species and of individuals in relation to environmental features, (2) biomass, (3) spacing within the community, and (4) patterns of interactions among species. Where there were recent reviews of a topic, I cited the review and relied heavily on it rather than citing and discussing individually the various papers contained in the review.

Nature of Herpetofaunal Assemblages

It has long been accepted that in general the numbers of species of reptiles and amphibians in the equable tropics is large and decreases toward the higher latitudes. This is exemplified by a comparison of species in two temperate and two tropical forests (Table 1) in which the tropical forests had greater species numbers than the temperate forests despite the fact that the fauna of the upper strata of the tropical forests was probably incompletely known. Porter (1972) has generalized that reptiles are restricted latitudinally and altitudinally primarily by cold, and that amphibians as a group are less cold-sensitive but tend to be restricted by dry conditions. Individual taxa do not necessarily follow these generalizations and may even show reverse trends.

The nature of the organization of species of "herps" (a reptile, amphibian, or both) in an assemblage, and the factors influencing such structure is an important aspect of community ecology. Heyer (1967) showed that four definite assemblages could be identified along a 24-km transect across the continental divide in Costa Rica which included both the Pacific and Caribbean slopes, an altitudinal range of 780 m, temperature ranges of 12°–33° C, annual rainfall of 1,700–3,800 mm, and six distinct vegetational

Table 1. *Comparison of the species numbers of amphibians and lizards in drained forests (A) and swamp forests (B) in a temperate (Michigan) and a tropical (Panama) area. Data from Heatwole and Getz (1960) and Sexton et al. (1964).*

Forest type	Amphibians	Lizards	Total
Michigan			
Oak-hickory (A)	2[a]	0	2
Hardwood swamp (B)	9	0	9
Panama			
Lowland rain forest (A)	5	6	11
Swamp forest (B)	10	6	16

[a] Excluding pond species.

formations. The distributions of the herpetofaunal assemblages were closely correlated with those of the vegetation zones, although some herpetofaunal assemblages spanned two vegetation zones. Individual species of herps spanned several or all of the assemblages, others were restricted to only one; however, there were areas of sharp faunal change between assemblages, and assemblages were well defined. The Pacific and Caribbean slopes were climatically different and had correspondingly different altitudinal demarcations of vegetation zones. Herpetofaunal zonation was not strictly altitudinal as samples from the same altitude on opposite sides of the divide represented different herpetofaunal assemblages. However, samples from the same vegetational zone represented the same assemblage. Heyer concluded that although the distributions of some species were limited by climatic factors, others correlated with specific microhabitats associated with particular vegetation zones. Thus, the hypothesis that zonation of herpetofaunal assemblages is primarily a direct climatic effect may be too simplistic and vegetation structure and type of habitats must also be considered.

Species Numbers

Comparisons of numbers of species among regional faunas or along latitudinal or moisture gradients could reflect differences in number of habitats in different regions, leaving the numbers of species per habitat relatively unchanged. Even comparisons among habitats may not be entirely valid. For example, deserts and forests are not structurally equivalent. Forests often have several structural layers (such as leaf litter, low vegetation, and canopy) whereas deserts have primarily a single shrub layer. Numbers of bird species correlate well with structural complexity of the habitat (MacArthur 1972) and the same may be true of herps as well. Structural considerations may also be important on a finer scale. Tropical forests usually have more strata (several canopy layers, for example) than do temperate ones; also, Heyer (1967) noted differences in the number of stories and their heights within his subtropical-tropical transect. There may be separate assemblages in each stratum of tropical forest and if so, the greater number of species there could be an expression of the greater number of strata rather than of climate or other factors per se. Consequently, to validly express latitudinal (or other regional) differences in numbers of herp species, it is important to use an equivalent community scale and numbers of layers of the habitat or to compare structurally similar habitats. There have been only a few studies treating herpetofaunal assemblages in a way amenable for such direct comparisons; most of these have dealt with deserts or with tropical forests or its component habitats.

Tropical Forests

Quantitative studies have been carried out on the herpetofauna of the lower forest stratum in tropical Guatemala (Stuart 1951, 1958), Panama (Sexton et al. 1964; Heatwole and Sexton 1966), the Philippines (Brown and Alcala 1961; Brown 1964), Borneo (Inger 1966), Africa (Scott, this volume), and Costa Rica (Scott 1976), and on the buttress faunas in Thailand and Ecuador (Heyer and Berven 1973) and Sumatra (Voris 1977), with sufficiently similar technique that at least broad comparisons can be made among areas. The number of herp species in a community depended on a variety of factors among which are altitude, climate, and specific geographic locality.

The greatest species numbers were found in the wet tropical lowlands, and regional differences were slight. However, there was a decrease in total number of lowland species with

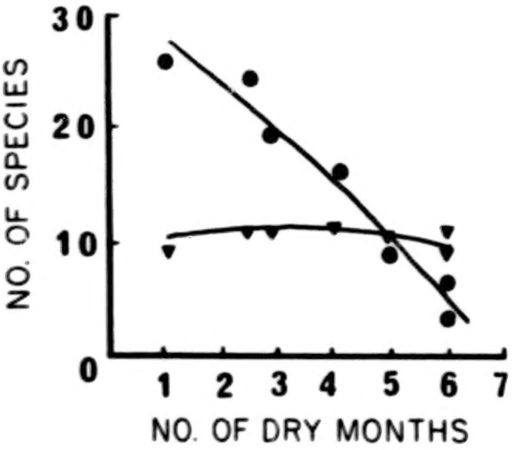

Fig. 1. Numbers of species of litter amphibians (dots) and lizards (triangles) in middle-American lowland forests with differing lengths of the dry season. Redrawn and modified from Scott (1976) with addition of data from Stuart (1958). Lines are eye-fitted.

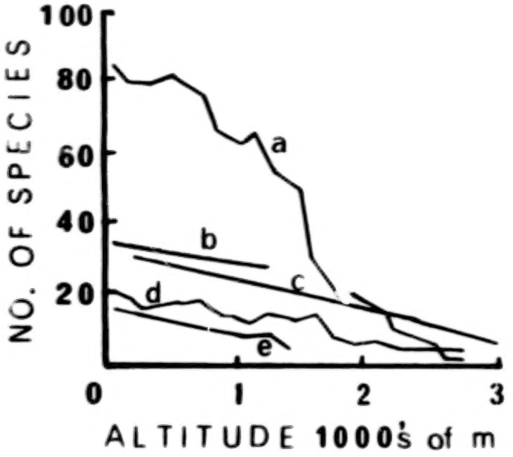

Fig. 2. Relation of tropical species-numbers to altitude. a = Costa Rican snakes; b = Costa Rican litter herps; c = Guatemalan forest herps; d = Costa Rican hylids; e = Philippine litter herps. Redrawn, modified, and horizontal axis corrected from Scott (1976) with data added from Stuart (1951, 1958).

increasing length of the dry season; this effect was especially pronounced in amphibians but slight, if at all, in lizards (Fig. 1).

Comparison of the assemblages on the buttresses in dry evergreen forest in Thailand and moist tropical forest in Ecuador is consistent with the moisture hypothesis. The dry evergreen forest had only a little more than a third of the number of species (12) as the moist tropical forest (34).

In a given geographic region and for all subgroups of the litter herpetofauna as well as for the herpetofauna as a whole, there was a tendency for decrease in species number with increasing altitude (Fig. 2). Since only a particular stratum of one habitat type (forest) was involved in these comparisons, the decreases in species number with altitude and dryness are not reflections of gross changes in habitat complexity but indicate decreases in the number of species in equivalent herpetofaunal assemblages.

A study of the total herp assemblages in Guatemala supports the conclusions based on analysis of the low-stratum assemblage alone; there was a decrease in species numbers with altitude (Fig. 2). However, in the Costa Rican transect of Heyer (1967), species numbers increased with altitude on both sides of the continental divide, perhaps reflecting community structural complexity rather than numbers per stratum or habitat. Thus the trends observed for particular habitats or strata do not necessarily apply on a gross community scale.

In the moisture continuum, species of the forest floor stratum probably decreased because fewer species (especially of amphibians) have adapted to the more extreme physical conditions. The altitudinal correlation is less easily explained and probably encompasses historical as well as climatic considerations. Scott (1976) suggested that differential ability of lowland species to invade uplands is partly responsible.

Differences between mainland and insular assemblages were also evident. The Philippines assemblages had fewer species than equivalent moisture conditions and altitudes in Costa Rica (Fig. 2). Scott (1976) suggested that the insular depauperateness, which is especially marked at higher altitudes, results from the fact that island montane faunas will equilibrate at a lower percentage of the available lowland species than will continental montane faunas because replacements by preadapted species will be slower on islands.

Inasmuch as various taxa of herps respond differently to environmental features, habitats in different areas may have different proportional representation of amphibians, lizards, and snakes. Amphibians seem to be especially moisture-sensitive. This was previously indicated by the great difference in numbers of leaf litter

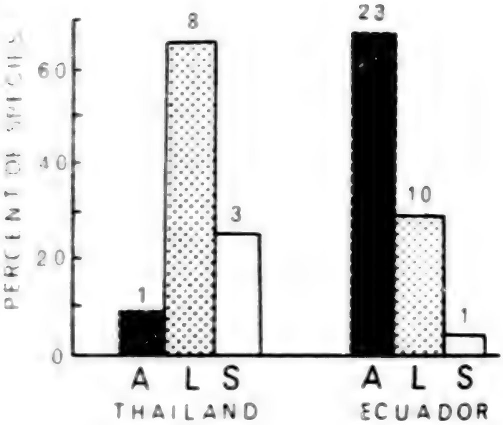

Fig. 3. Proportion of the buttress herpetofauna consisting of amphibians (A), lizards (L), and snakes (S) in Thailand and Ecuador. Numbers above histograms indicate actual number of species. Data from Heyer and Berven (1973)

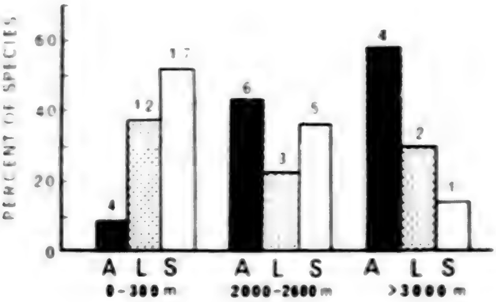

Fig. 4. Proportion of the total herpetofauna consisting of amphibians (A), lizards (L), and snakes (S) in Guatemalan forests: Tropical Dry Forest (0–300 m), Oak-Pine Forest (2,000–2,600 m), and Pine Cypress Forest (> 3,000 m). Data from Stuart (1951, 1958). Numbers above histograms indicate actual number of species.

frog species between forests with long dry seasons and those with short ones, compared to the relatively small differences in numbers of lizard species in the same forest floors (Fig. 1).

The composition of the buttress herpetofauna differs greatly between the Ecuadorian and Thailand forests; the proportion of amphibians is very low in the drier Thailand forest, but high in the wetter Ecuadorian one (Fig. 3). Heyer and Berven (1973) suggested that these differences arise in part because in the New World the genus *Eleutherodactylus* (which is heavily represented in the Ecuadorian buttress fauna) has direct development and is thus freed from standing water for reproduction and can consequently invade habitats closed to most amphibia; in Thailand this niche has been occupied by several lizards in the absence of frogs with direct development. The similar changes of proportional representation by amphibians along moisture gradients in the New World would suggest, however, that a sensitivity to moisture other than in terms of mode of development may also be involved.

In contrast to the sensitivity to moisture conditions, amphibians are less markedly influenced by altitude and latitude than are reptiles (cf. Costa Rican snakes and hylids in Fig. 2).

In the Guatemalan forests, increasing altitude resulted in a proportionately greater reduction in reptiles than in amphibians and the percentage of the assemblages represented by amphibian species increased with altitude (Fig. 4). In contrast, an increase of 1,200 m altitude in Costa Rica, although it reduced both the numbers of litter lizards and amphibians, did not greatly alter the proportion of the two (Fig. 5). Heyer's (1967) transect revealed slight variations in

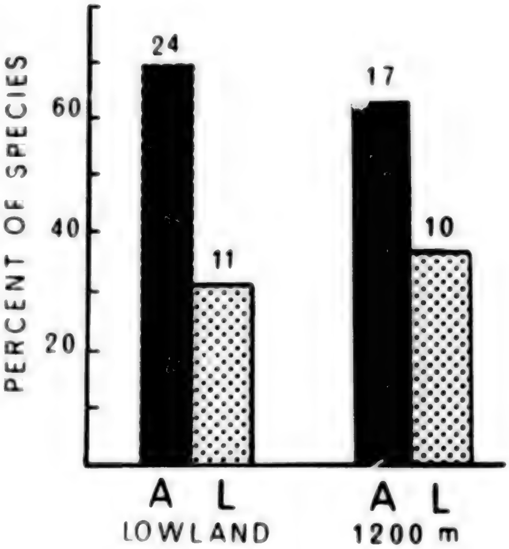

Fig. 5. Proportion of the combined numbers of lizard and amphibian species consisting of amphibians (A) and lizards (L) from wet forests in Costa Rica at different altitudes. Numbers above histograms indicate actual number of species. Data from Scott (1976).

species composition from one assemblage to another (amphibians, 37-54%; lizards, 20-27%; and snakes, 25-39%) with no consistent relation to climate or altitude. Again, one would have to analyze the separate habitats of the structurally different vegetation types for full assessment to be made of the Guatemalan data and of Heyer's transect.

In summary, the total number of species in herpetofaunal assemblages decreases with increasing latitude and altitude, with decreasing availability of moisture, and with greater insularity. The altitudinal and latitudinal effects are often influenced more strongly by decreases in reptiles than by those of amphibians, whereas the effects of moisture are the reverse. These trends can be demonstrated independent of gross changes in habitat complexity (layering), but are not always exhibited on the gross level, probably because of the added influence of community complexity.

Deserts

Numbers of species of amphibians in deserts are low and most work has concentrated on reptiles only. Pianka (1967), in a study of North American desert lizard assemblages, found that ecological time, spatial heterogeneity, length of growing season, and amount of warm-season productivity were related to the number of species occurring in an area. The most important factor was spatial (mainly vegetative) heterogeneity of the environment. He suggested that the effect was indirect and that climatic variability allows the coexistence of many plant life-forms, the variety of which in turn controls lizard species-number. Thus, the prime control factor was postulated to be climatic-vegetative. However, Pianka actually treated localities rather than habitats and part of the heterogeneity within a given locality might reflect proximity of several types of desert habitats. In a later study (Pianka 1971) of the Kalahari Desert, he found that the most important variables influencing lizard species-number seemed to be plant species diversity and mean annual precipitation. The Kalahari and American deserts were poor in number of species per locality compared to the Australian deserts (Table 2). Pianka (1969) attributed the exceptional species-numbers of Australian deserts to (1) lizards usurping ecological roles played by some worms, insects, snakes, and mammals in North America (he considered the desert mammal and snake faunas impoverished in Australia), (2) greater temporal partitioning because of the milder and more constant Australian desert climate, (3) more narrow specialization by Australian desert lizards, and (4) greater spatial heterogeneity in Australian deserts because of an interdigitation of different habitat types, including one type, "spinifex" (*Triodia*), which is unique to Australia. Cogger (1961) previously pointed out the importance of *Triodia* in this regard. This grass has a unique life-form, occurring in dense clumps with sharp spike-like leaves interlacing and facing outward. In addition to providing a formidable defense against large predators for animals small enough to pass through the interstices, it provides an unusually equable microclimate. Diurnal humidity is higher and temperature lower than elsewhere, and shade is dense. A large number of "desert" reptiles are closely dependent on *Triodia* for conditions suitable to life and probably could not survive without this plant. Cogger (1961) argued that the fact that the life form of *Triodia* is unique to Australian deserts and has its own special reptilian fauna, may account for much of the greater species richness of Australian deserts.

Table 2. *Mean species density of lizards with different habitats and time niches in various localities in deserts of three continents (after Pianka 1971).*

Habitat and habits	North America	Kalahari	Australia
Diurnal, terrestrial	5.4	6.3	14.4
Diurnal, arboreal	0.9	1.9	2.6
Nocturnal, terrestrial	1.1	3.5	7.6
Nocturnal, arboreal	0.0	1.6	2.6
Fossorial	0.0	1.4	1.1
Total	7.4	14.7	28.3

As mentioned above, the real difficulty in evaluating any of the above discussion is that localities are the units of study, not habitats. As Pianka (1969) noted, a given area may have an interdigitation of habitats; part of his discussion is based on the fact that such interdigitation is greater in Australia and that each habitat has its own specialized lizard fauna as well as more ubiquitous ones. Unfortunately, he provided a breakdown by habitat only for the Australian deserts. Pianka recognized three major habitats, *Triodia* or sand-plain, mulga or shrub-acacia, and sandridges. If it can be assumed that in each American and Kalahari locality only one habitat was represented, the number of species per locality can be compared with the number per habitat type in Australia. In the Kalahari, 12 to 18 species may occur at the same locality (Pianka 1971), whereas in North America the number may be 10 or less (Pianka 1967). The mulga and sandridge habitats in Australia may contain up to 20 species each, "spinifex" up to 22, and a large number of species are not definitely assigned to any of these habitat types (Pianka 1969). Thus, it appears that even when habitat rather than localities is considered, Pianka's conclusion that the Australian deserts are richer in species than the American or Kalahari deserts is valid. If the African and American localities encompass more than one habitat, the differences would be even greater.

If one compares the species densities of lizards in deserts with that in tropical grasslands or the ground stratum of lowland forests (which are as similar structural units as can be found for comparisons between such different habitats) it is clear that deserts and tropical habitats are about equivalent; mean species densities of desert lizard species per habitat are 7.4 and 14 in the American and Kalahari deserts, respectively, about 10 for a variety of Central American forests (Fig. 1), and 6 in the grass stratum in the savannahs of the Venezuelan Llanos (Staton and Dixon 1977). This equivalence holds up although most of the deserts discussed here are at higher latitudes than are the tropical forests. In the special situation of Australia, desert habitats (20-22 species of lizard per habitat) are even richer than those of the forest floor.

One can conclude that within broad latitudinal limits and over a great range of moisture conditions, the number of lizard species in the lower strata of mainland habitats do not vary greatly, in marked contrast to that of amphibians or the herpetofauna as a whole. The greater number of species in forests would seem to reflect the additional assemblages occupying the strata found in forest but not in desert, rather than differences in the number of species in the stratum that both habitats share.

The desert environment is relatively erratic and unpredictable, and one might suspect that the large year-to-year fluctuations in the environment might be reflected in changes in the numbers of species over time. Support for this view was obtained by Whitford and Creusere (1977) who found that during wet periods species numbers in some Chihuahuan Desert localities increased because of an expansion of suitable habitat and an influx of immigrants and transients from more mesic habitats. During dry periods these died out again.

Number of Individuals

It has been noted that number of herp species is greatest in the wet tropical lowlands of mainlands but that it decreases with increasing latitude, altitude, aridity, and insularity. Do the same or different trends apply to numbers of individuals? Few sufficiently quantitative studies have been carried out to permit evaluation; they include studies in the lower stratum of tropical forests of Panama, Costa Rica, Borneo, Africa, and the Philippines (reviewed by Scott 1976 and this volume). A surprising but consistent result was that the number of individuals increases with increasing altitude up to a certain level (Fig. 6), but thereafter decreases again, i.e., the greatest standing crops of herps occur at intermediate elevations rather than in the lowlands. There was also a difference between Asian and middle-American localities; individual numbers were lower in Asia. The numbers of individuals also decreased with increasing length of

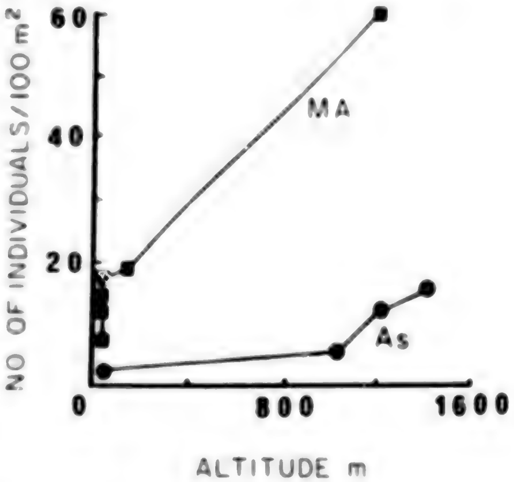

Fig. 6. Relation of numbers of individuals of leaf litter herps in tropical forests of middle America (MA, squares) and Asia (As, dots) at different altitudes

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the dry season among American tropical lowland sites (except that one locality, Silugandi, Panama was unusually high; Scott 1976: Table 1), and at the Costa Rican localities numbers of individuals were lower in the dry than in the wet season and lower on slopes than on flat terrain. Scott (1976), although not ruling out biotic factors such as predation, suggested that all these differences were related to general productivity limits in the forest floor. He suggested that dryness (whether due to seasonal or edaphic factors) reduces productivity and that litter production may be greatest at intermediate elevations and greater in middle America than in Asia. Such productivity differences would filter through the food chain and eventually influence herps. Whitford and Creusere (1977) found that in the Chihuahuan Desert lizard densities varied directly with rainfall-induced changes in productivity and relative abundance, and activity of arthropods.

Insularity is another factor influencing densities of herps. It has been documented repeatedly that the number of species is usually smaller on islands than in equivalent mainland habitats and that the number of species on islands is a function of island size (MacArthur and Wilson 1967). However, the influence of insularity on numbers of individuals has not been studied often. Case (1975) found that on the islands in the Gulf of California, lizard numbers were inversely related to number of lizard species. The reasons for such density compensation were concluded to be differences in predation intensity, insect productivity, and possibly reduced competitive interference on small, isolated islands.

Equitability

A flurry of activity related to the concept of species diversity appears in the literature of recent years and various diversity indices have been developed. Although a few studies have applied these techniques to herpetofaunal assemblages (Lloyd et al. 1968; Heyer and Berven 1973), this aspect will not be reviewed here. I concur with Hurlbert (1971), DeBenedictus (1973), Peet (1975), and others that the concept of species diversity as expressed as an index is often biologically meaningless. It embodies two separate concepts (species richness and equitability) and a synthesis of the two into a single index has little value. It is preferable to look at the two components of species diversity separately. One of these, species richness, has been previously examined, and the other, equitability, will be treated now. Equitability indicates how the individuals of an assemblage are distributed among species. If all species contain the same number of individuals the apportionment is equitable. If some species are abundant and others extremely rare, the distribution is highly inequitable. I will employ a graphic method of presentation in view of the frequent inappropriateness of equitability indices (Peet 1975).

The observation that some tropical forests have many species has led to the popular conception that no one species is common, i.e., that equitability in the tropics is high, and all species are rare. For example, Maiorana (1976), in a review including reptiles and amphibians, stated: "There are many species in the tropics, but generally individuals of any one of them are rare." Although this may be true for some organisms, there is abundant evidence that it is not true for amphibians or reptiles. When latitudinal comparisons are made of the population densities of herp species, it is often true that the highest population densities are encountered in tropical species (see reviews by Tinkle 1967; Turner and Gist 1970; and Heatwole 1976). There are one or a few species in each tropical herpetofaunal assemblage that are extremely abundant and account for a large proportion of the total number of individuals of the assemblage; the remaining species are relatively uncommon, i.e., equitability is low. In fact, in all but 2 of the 10 assemblages from various altitudes (lowland to 1,450 m) and localities (Panama, Costa Rica, Borneo, Philippines) reviewed by Scott (1976: Fig. 6), the most abundant species was represented by twice the number of individuals of the second-most abundant species; sometimes the differences were sixfold or more and the most abundant species contained more individuals than the rest of the species of the assemblage combined. The two exceptions were the only two assemblages represented by small samples, and even those showed considerable differences in abundance among species. Turner (1961) plotted the numerical abundance of snakes in Panama and California against their rank in abundance and got similar curves for both areas.

Although all the assemblages reviewed by Scott (1976) were inequitable, some were more inequitable than others. Equitability decreased from the lowlands to the highlands in the two areas (Costa Rica, Philippines) for which sufficient altitudinal data were available. Although there was a decrease in numbers of species with altitude, there were more individuals at the intermediate than at low altitudes. It appears that the altitudinal reduction in rare species was more than compensated by an increase in numbers of individuals of the commonest species. There was also a trend for more equitable distribution of individuals among species in the wetter as opposed to the drier American lowland assemblages, although small samples from some areas prevented a rigorous analysis. However, the data of Heyer and Berven (1973) provide a better contrast between an assemblage (buttress fauna) from two forests differing in moisture characteristics. In dry tropical faunas (Thailand) equitability was low; the most abundant species accounted for well over half the total number of individuals, whereas in Ecuadorian wet tropical forest the distribution of individuals among species was unusually equitable. In fact, this assemblage has the highest equitability of any herpetofaunal assemblage of which I am aware. The six most common species collectively accounted for only 50% of the total individuals and the most abundant one for only 10% (Fig. 7). Although moisture conditions may have influenced these differences in equitability, it is premature to draw firm conclusions. The Thailand and Ecuadorian forests differed in ways other than moisture and continent; in Thailand the assemblage was dominated by lizards, in Ecuador by amphibians (but note that Lloyd et al. 1968 found equitability to be greater among lizards than among frogs). Furthermore, the assemblage of the Ecuadorian wet tropical forest was much more equitable than any from lowland wet forests in middle America.

The graphic portrayal of abundances of Chihuahuan Desert lizards gave equitability curves similar to those for tropical forests, i.e., the most abundant species often were twice as dense as the next most abundant species (Whitford and Creusere 1977). Considering all the above studies collectively, it is doubtful whether moisture plays a great role in influencing equitability.

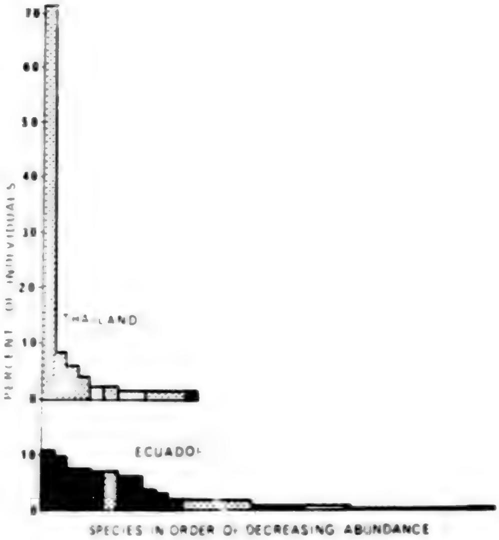

Fig. 7. Equitability in the herpetofauna of buttresses in forests in Thailand and Ecuador. Black dots on white = lizards; white dots on black = amphibians; open histograms = snakes.

On the basis of a study of Sarawak frogs, Inger (1969) implied that organization in amphibian assemblages may follow definite patterns in particular kinds of habitats, but that the role of a particular species may change from one locality to another, i.e., as one species declines in numbers, its place may be filled by an ecologically similar one that might be otherwise less numerous. He felt that the relative constancy of the frequencies of ecological types (not necessarily the same species) from stream to stream and the similarities in equitabilities meant that a given species could be added to or removed from a community without greatly affecting community structure because of the resulting changes in other species. He further hypothesized that the physical environment was ultimately responsible for community structuring in that it determined the success of particular ecological types (each of which might include a number of species). It is possible that the structuring of ecological types is determined by the physical environment, but that biotic factors influence which species of a given type predominates in the assemblage.

In summary, herpetofaunal assemblages are generally relatively inequitable; equitability decreases with altitude but with no consistent relation to moisture. It is important to obtain additional empirical data on this topic from a variety of geographic regions and across environmental gradients of different kinds. Data are at present insufficient to formulate a general theory of either the significance of equitability differences or identifications of causal factors. However, it has been suggested that particular environments determine the structuring and equitability of assemblages, and that within that structure species may be interchangeable. Clearly, much empirical data on this topic is still needed.

Biomass

A given area of habitat could theoretically support either a large number of small reptiles or a smaller number of large ones. Thus, data on numbers of individuals, as valuable as they are, do not tell the whole story. It is also essential to know the collective weight (biomass) of herps occupying a unit of habitat if community structure is to be fully understood. Although biomass values have been reported for a few individual species of herps (see review by Heatwole 1976), biomass of entire herpetofaunal assemblages have scarcely been studied (see Bury and Fitch, this volume). The work of Barbault (1970) is an exception; the mean annual biomass of the snakes (37 species) in an African savannah was 150 g ha and the greatest values occurred during the wetter parts of the year. In the same season, there were differences between habitats (plateaus, slopes, low ground, and burned vs. unburned areas). Burned areas had a relatively low biomass compared with unburned but otherwise equivalent regions. Most of the differences among habitats were attributable to frog-eating species whose biomass changes followed those of their prey species (Fig. 8); lizard-eating species also showed biomass changes correlating with those of their prey.

Type of habitat may be important in biomass stability. Barbault (1967) found that total biomass of ground-dwelling lizards showed large seasonal fluctuation; low values occurred following fires after which they rose and reached a peak by the end of the rainy season; by contrast arboreal lizards showed little seasonal change in biomass. Lizard biomass varied by as much as twofold between comparable seasons of different years. Amphibian biomass depended largely on moisture conditions (Figs. 8, 9).

These two studies illustrate the importance of biomass studies. In the terms of the structuring of such assemblages, it would seem to be important to evaluate the distribution of biomass among species, i.e., look at biomass equitability. Such an approach may add a new dimension to the study of herpetofaunal assemblages and might open up fruitful avenues of research.

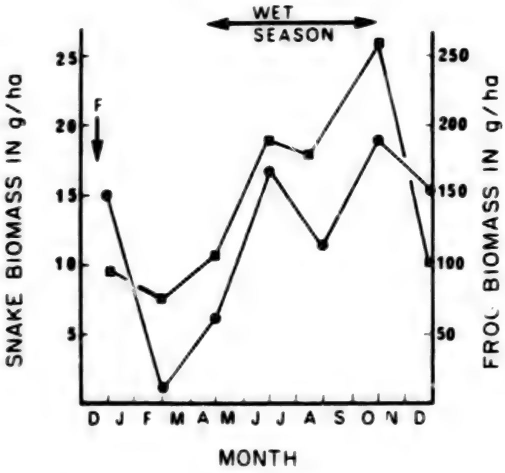

Fig. 8. Changes of mean biomass of frogs (squares) and frog-eating snakes (dots) in a savannah in Ivory Coast. F and arrow indicates fire. Redrawn from Barbault (1970).

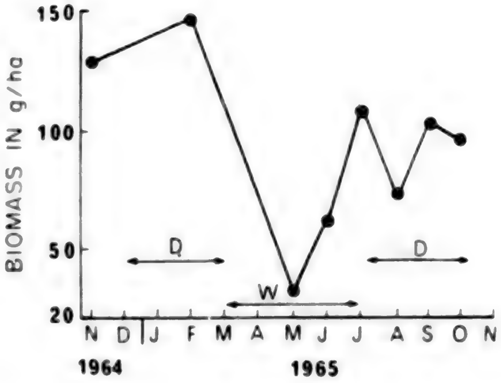

Fig. 9. Changes in amphibian biomass in a savannah in Ivory Coast in relation to the wet (W above arrow) and dry (D's above arrows) seasons of 1964-65. Data from Barbault (1967).

Spacing

The species of a herpetofaunal assemblage are not randomly distributed in space either horizon-

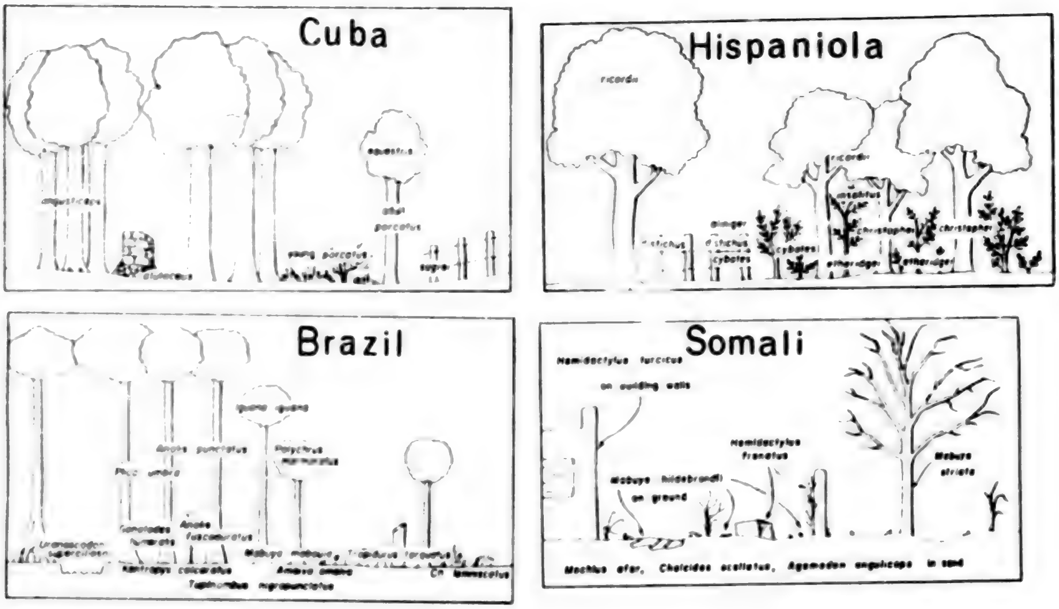

Fig. 10. Generalized schemes of spacing of lizards of the genus *Anolis* (upper two squares) and total lizard fauna (bottom two squares) in four regions. Redrawn from Collette (1961), Gans et al. (1965), Rand and Humphrey (1968), and Rand and Williams (1969).

tally or vertically; they occupy discrete microhabitats. This being true, it is presumed that the greater the spatial (structural) diversity in a habitat, the greater the number of species which can coexist there. Many investigators have qualitatively appreciated spacing patterns among herps, and diagrams indicating the nature of such spacing have appeared for a number of assemblages (e.g., Fig. 10). Where vegetation structure permits, there is often a subterranean assemblage, a leaf litter or cryptic assemblage, a low bush assemblage, a tree trunk assemblage, and one or more canopy assemblages. Where there is horizontal heterogeneity, different assemblages may occur in the more open areas than in the closed canopy areas (Fig. 11). Sea snakes show vertical and horizontal spacing (Fig. 12).

Heatwole (1977) reviewed the role of habitat selection in the spacing of reptilian assemblages and concluded (1) that spacing may in some instances arise from interspecific differences in response to the geometry of the physical environment and in others from differential responses to spatial variation in microclimatic factors, (2) that expressions of habitat selection are often modified by the presence of other species in the same general habitat, and spacing is correspondingly affected (habitat shifts), (3) that intraspecific differences in habitat selection may tend to result in spatial separation of sexes or ontogenetic stages, but (4) that intraspecific aggression is sometimes involved in causing or maintaining such separations.

The spatial separation of the different sexes or the young from adults might maximize the number of individuals that can be maintained within a given habitat and consequently influence equitability. It would be interesting to ascertain whether common species more often have intraspecific differences in microhabitat than do rarer ones.

Biotic Interactions

Space is not the only biologically relevant dimension of a species' niche. A variety of other aspects such as food, shelter, and basking sites is also involved and the structuring of assemblages may depend on the ways species interact in partitioning such resources. Milstead (1972) suggested that for a given biome, there are a large number of finite niches, filled in different localities by

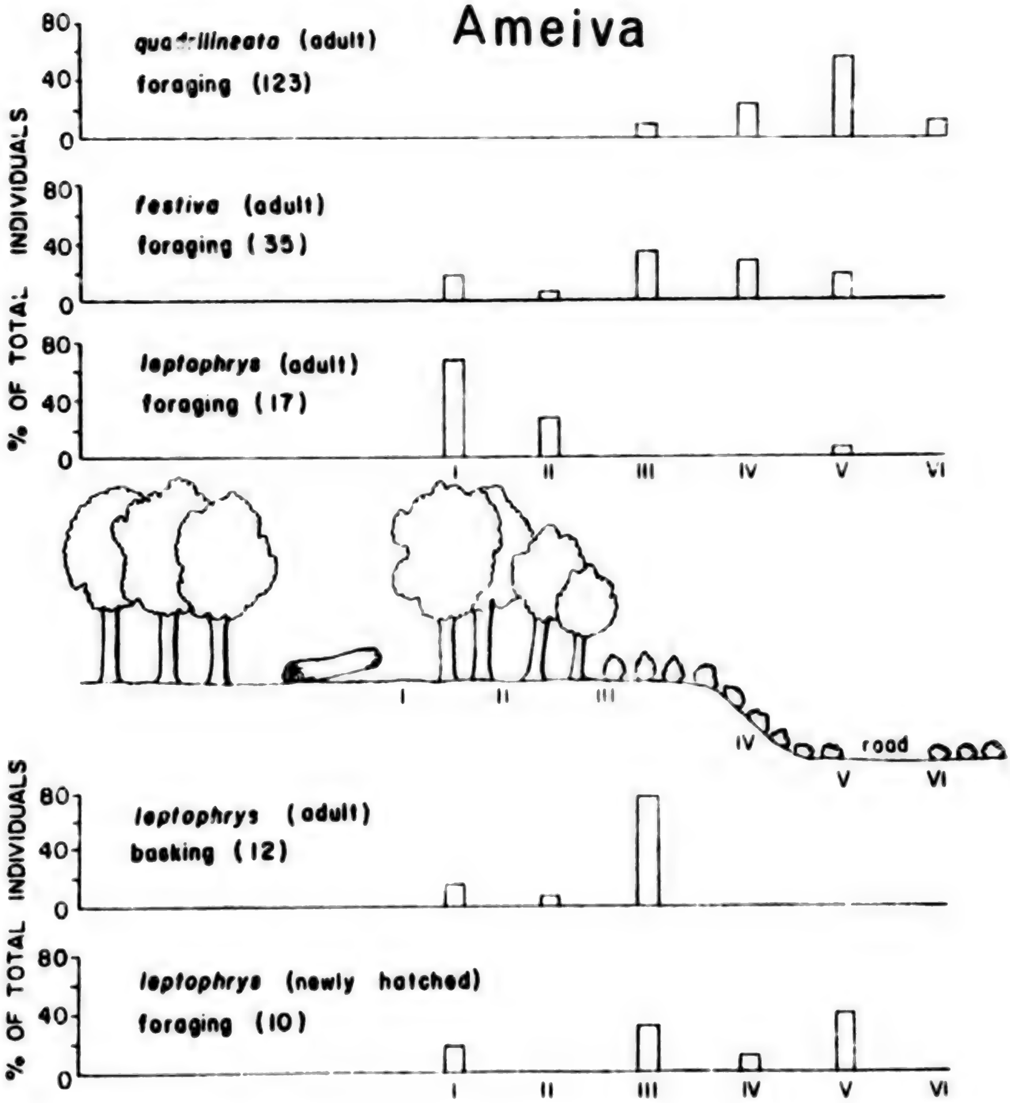

Fig. 11. Horizontal changes in habitat of lizards of the genus *Ameiva* in Costa Rica. Note the relative frequencies of individuals in the various habitats – histograms marked with Roman numerals correspond to the areas of the habitat profile of the same number. Redrawn from Hillman (1969).

convergent ecological equivalents that partition resources in similar ways.

Much of the research in resource partitioning has involved species-pairs or small groups of species rather than whole assemblages. However, the principles established by the study of small units are probably applicable to larger ones as well. Consequently, it is appropriate to briefly summarize the main points arising from these as well as from more synthetic studies (for lizards see reviews by Milstead 1961; Pianka 1973; Schoener 1974, 1975; and the studies of Milstead and Tinkle 1969; Marcellini and Mackey 1970; Schall 1973; Hurtubia and DiCastri 1973; Scudday and Dixon 1973; Huey and Pianka 1974; Huey et al. 1974; Fitch 1975; Simon and Middendorf 1976; Rose 1976; Talbot 1977; for snakes see Fitch, Brown and Parker, and Reynolds and Scott, this volume; for salamanders see Jaeger 1972, 1974; Bury and Martin 1973; Fraser

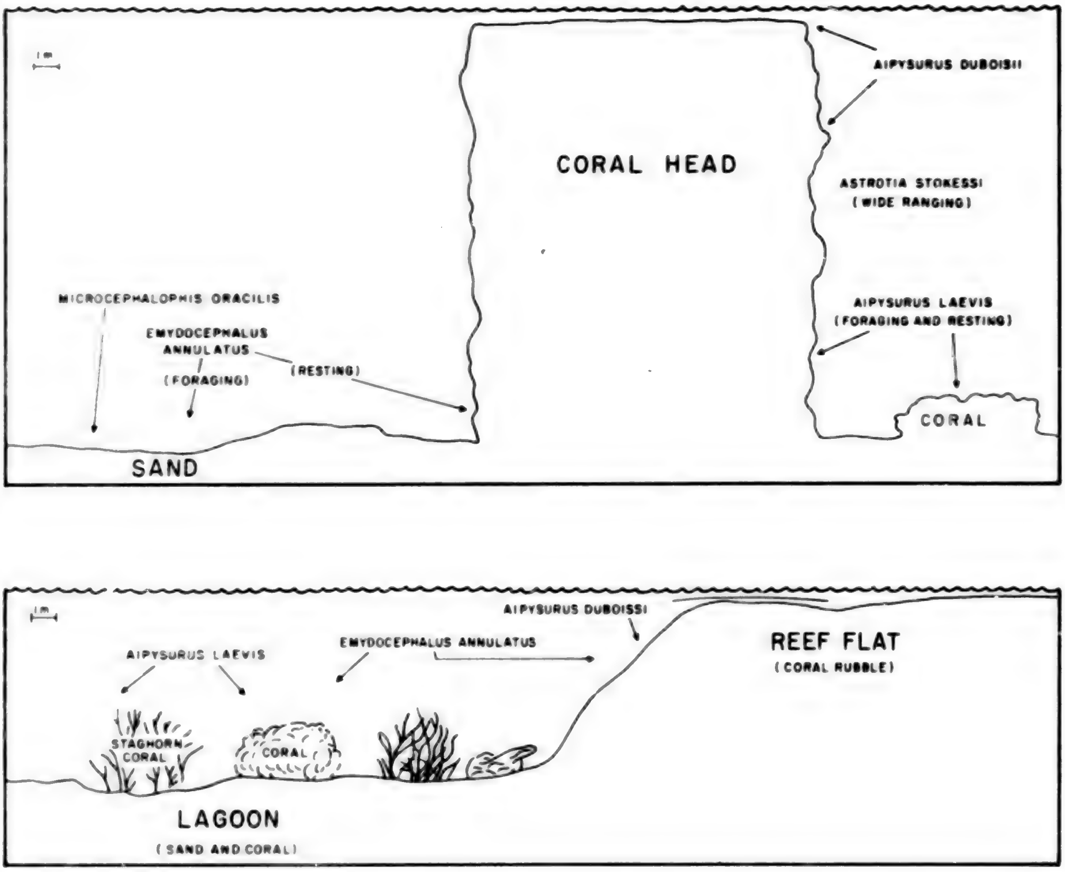

Fig. 12. Spatial separation of sea snakes on two reefs in the Coral Sea. Modified from Heatwole (1975).

1976*a*, 1976*b*; frogs are treated separately later). Resource partitioning is achieved by (1) spatial separation (also see Spacing), (2) differences in size among species, especially head size and its attendant influence on the size of prey which can be eaten, (3) differences in types, or (4) size of prey accepted or selected, and (5) the time in which activity occurs. Intraspecific differences paralleling the above-mentioned interspecific ones may also occur and result in a finer scaled partitioning. In some lizards allochronic seasonal and spatial activity may separate adults and juveniles (Whitford and Creusere 1977; Creusere and Whitford, this volume).

It is important to assess the relative importance of the various niche dimensions in separating the members of assemblages in different communities. Pianka (1973) did this for desert lizards and showed that food is a major factor separating niches of North American species, whereas in the Kalahari, food niche separation is slight and differences in space and time are considerable. All three of these dimensions are important in separating the niches of Australian desert lizards.

Among the anoles, it would appear that separation in place and in food niches are the most important. Schoener (1975) suggested that in this group intensity of competition appears to (1) decrease with increasing differences in size between species; (2) be greater for a given size difference if the competitor is larger than if it is smaller; and (3) decrease at nonconstant rates, so that at near complete size similarity decline in intensity is more rapid for smaller than for larger competitors. It appears that the size-structure of a herpetofaunal assemblage may be an important characteristic to study, especially when coupled with information on microhabitat and on food habits (i.e., does an assemblage have an array of different-sized species in each trophic and habitat category but few similar-sized ones in a given one?). Where anoles are released from competition from congeners (as on some islands) niche expansion occurs along the habitat, perch height, microclimate site, and prey size axes (Lister 1976).

Frogs, like lizards, tend to be generalized insectivores and many of the above considerations regarding niche separation may be expected to apply to them as well. The frog genus *Eleutherodactylus* is the ecological equivalent of the lizard genus *Anolis;* both are exceptionally large genera, have explosively radiated in tropical America, and are often represented by a number of species in the same assemblage. Like the anoles, *Eleutherodactylus* shows spatial segregation. Heatwole (1963) indicated that two species were horizontally and vertically separated in Venezuelan cloud forest; *E. terraebolivaris* occupied the tree falls, roadsides, and other open, second growth, and *E. cornutus* occupied the closed, shaded areas. Furthermore, the former leaves the litter at night and climbs up on vegetation for its activity period whereas the latter remains on the forest floor. Similarly, Cintron (1970) found that although there was considerable spatial overlap among the *Eleutherodactylus* species in Puerto Rico cloud forest, certain species tended to occupy particular strata or microhabitats (e.g., one was found primarily in bromeliads in trees, another mainly inside of the petioles of fallen palm fronds, and a third mostly under such petioles or other debris); a large species tended to feed on ants and the smaller species on small beetles. Drewry (1970) found that although the time of calling strongly overlapped, there were differences in peak of calling activity. It appears that spatial isolation is the major separating factor and a lesser difference in food and activity niches is also operative.

Inger and Marx (1961) examined the food habits of 20 species of African amphibians and found that there were interspecific differences in the food niche, and selectivity was based primarily on differences in size range of prey; there were interspecific differences in the size of prey eaten, but within a species prey size did not vary greatly with size of frog.

Heyer and Bellin (1973) examined space niche overlap (as indicated by horizontal and vertical location and vegetation type occupied) in five sympatric *Leptodactylus* in Ecuador. Three of the species had broad niches and two had narrower ones. There was considerable overlap among some of the species (Table 3). *Leptodactylus discodactylus* overlapped little with other species, in part because of distinctive calling sites used by males of that species. The species with high overlap in the spatial (habitat) niche belong to different species-groups, and Heyer and Bellin suggested that aspects other than habitat may be more important in niche differentiation among them. In any event, it is clear that although some species tend to be spatially segregated, not all are.

Dankers (1977) studied an assemblage of 18 species of frogs around a pond in eastern Australia and found that almost all were separated by differences in seasonal or daily activity period, location around the periphery of the pond, or within a given area by microhabitat. One species-pair that showed little temporal or spatial overlap differed greatly in size. (For a study of the temporal and spatial patterns of a North American frog assemblage, see Wiest, this volume.)

Inger and Greenberg (1966*a*) studied three species of *Rana* in Sarawak and found that spatial separation was slight and not the factor involved in their continued coexistence. Niche overlap was extensive and although coexistence is

Table 3. *Niche breadth and niche overlap values for five species of* Leptodactylus *from Ecuador (from Heyer and Bellin 1973).*

		Niche overlap			
ies	Niche breadth	*L. knudseni*	*L. mystaceus*	*L. pentadactylus*	*L. wagneri*
discodactylus	1.29	0.26	0.26	0.27	0.26
L. knudseni	2.54	–	0.99	0.63	1.00
L. mystaceus	2.36		–	0.68	0.99
L. pentadactylus	1.44			—	0.64
L. wagneri	2.53				

indefinitely maintained, some competition seemed to be occurring as removal of a species resulted in increases in the density of remaining ones. They suggested that maximum population levels are fixed by intraspecific competition, a mechanism also postulated by Dankers (1977) for one of his overlapping species-pairs.

The above studies suggest that frogs are separated by much the same factors as are lizards. However, it appears that in lizards spatial components tend to be more important than in frogs but that frogs rely more heavily upon temporal separations. Ascertaining whether this impression is correct must await further comparative studies. However, it appears even at this rudimentary stage that the eleutherodactylines more closely resemble lizards in tending toward spatial segregation.

Thus far, only adult amphibians have been considered. However, given bodies of water may contain a variety of species of larvae and their potential interactions must be considered. This topic has been recently reviewed (Heyer 1976). Heyer stated that "available evidence indicates that communities of tadpoles represent nothing more than a collection of species coexisting as larvae. A tadpole community is not an integrated whole; biological interactions within the community are not important evolutionarily; there is no natural selection operating directly to integrate or partition the community." He arrived at these conclusions despite the finding of spatial and temporal separation among species, and even habitat shifts in the presence of other species, sometimes interpreted in competitive terms by the authors he cited. Heyer based his argument on the facts that (1) predation is a major organizing influence in tadpole assemblages, (2) in some instances different years result in different temporal or spatial patterns among species, (3) that he could formulate alternate hypotheses to account for presumed competition, and (4) that models had been constructed which permitted coexistence without competitive exclusion. He suggested that differences in habitat occurred as an adaptation to particular environments developed in isolation from presently coexisting species; spatial or temporal separation may arise from competition for calling or oviposition sites by adults of territorial species. He explains habitat shifts of a species when in the presence of another as a density effect independent of competition.

In critique of Heyer's views it must be mentioned (1) that although year-to-year differences in breeding times and places and with different species mixes might occur, it does not mean that such species compete at no time, nor that such competition, even if occurring occasionally, would lack selective significance in adjusting long-term trends in habitat selection or breeding phenology; (2) that ability to formulate alternate hypotheses does not necessarily disprove a pre-existing one; and (3) that models are merely highly organized, formal hypotheses and do not constitute evidence of anything. One could construct any number of models at will and arrive at any conclusions desired. Models are justified in that they stimulate empirical testing of the ideas they embody, but as an end in themselves are mere mental exercises. Heyer's main contributions, other than the empirical data on several tadpole assemblages, were the demonstration of similarity in feeding habits of various overlapping species, the providing of stimulating alternate hypotheses on organization of tadpole assemblages, and in questioning the dogma that competition is the main selective agent influencing habitat selection in larvae. In so doing, I feel he went too far in making unwarranted, blanket generalizations and in setting up the counter-dogma of no interactive affects. Further research involving detailed comparative studies of tadpole assemblages testing his ideas are clearly desirable.

Life History, Reproduction, and Community Structure

Maiorana (1976) recently reviewed the literature on the relation of life history variables to community structure, including assemblages of reptiles and amphibians. She emphasized that seasonal, temperate-zone environments select for breeding only at the most favorable time for juvenile survival. Equable tropical environments permit a greater seasonal spread of reproduction, and in general tropical lizards are characterized by early maturity, multiple but smaller clutches, and reduced life expectancy in comparison with temperate ones. However, lizards from seasonal tropical environments have reproductive strategies similar to those of lizards from the equable tropics and she suggested that tropical seasonality is not as severe as is that of temperate regions. She concluded that (1) abiotic factors may be important in shaping the reproductive patterns of temperate lizards (length of favorable season and uncertainty in the quality of that season), (2) predation is probably important as a selective force in the life history patterns of tropical lizards but in seasonal tropical environments abiotic factors influence timing of reproduction, and (3) competition is not an important selective force in life history patterns. If these conclusions prove to be true, then it seems that in lizards, spacing and habitat selection may be influenced by competition but life history strategies more by seasonality and predation. However, Inger and Greenberg (1966*b*) suggested that in equable tropical forests, lack of seasonal restriction and the resulting continuous breeding of lizards may lead to increased interaction among species. Separation in space may consequently be a reflection of such interaction.

Amphibians differ considerably from lizards in some regards. Maiorana (1976) noted that many species are restricted to standing water or its vicinity for reproduction and suggested that predation pressures on larvae and competition among them in such aquatic environments are probably intense (but see Heyer 1976). In the equable tropics, conditions favoring reproduction are extended throughout most of the year and amphibians can become temporally segregated, using breeding water sequentially in time and hence avoid larval competition. Consequently more species can coexist than in seasonal environments where favorable conditions do not persist long enough for temporal segregation of more than a few species. It is possible this is the factor which is responsible for the reduction of species numbers of frogs with increasing length of dry season noted in the section on species numbers. If coexistence or lack thereof is determined primarily by interaction at the larval stage in amphibians, rather than competition at the adult level, it would explain why adult amphibians seem to show less spatial separation but greater temporal segregation in breeding than lizards.

Heyer (1976) concurred that the larval stage may be the bottleneck as far as population densities are concerned. He suggested that predation and weather-influenced uncertainties, such as drying or freezing of ponds, cause high mortalities and that adult population levels consequently are below the carrying capacity of the environment, except for possible scarcity of breeding or oviposition sites in territorial species. Creusere and Whitford (1976) provided data supporting this idea.

Regardless of the factors involved, if it is true that high larval mortality results in lack of competition among adults, it explains relative lack of spatial separation among adults of different species in some amphibian groups and also explains the apparent importance of spatial separation in direct developers (see Biotic Interactions). The genus *Eleutherodactylus* has direct development and is thus freed from the high mortality imposed by aquatic environments. Predictably, the little information available suggests that like lizards, this genus shows considerable spatial segregation among adults of different species. These ideas have not been rigorously documented empirically; the data are sufficient only to be tantalizingly suggestive. Detailed empirical studies of comparative ecology and life history of various tropical amphibians, especially those with direct development, must be carried out before firm conclusions can be reached as to the role of life history variables in structuring of assemblages.

In addition to the insectivorous frogs and lizards discussed above, herpetofaunal assemblages may contain herbivorous lizards and turtles, or carnivorous members from all taxa, especially snakes, that may prey upon other herps. Most work has been done on rather generalized insectivores and the way that they segregate ecologically. Trophic structuring involving herbivorous or non-insectivorous predators in herp assemblages is a topic scarcely explained. However, Walters (1975) showed that different species of amphibian eggs and larvae have different palatabilities to their amphibian and reptilian predators. In the field there was sometimes intense predation and a negative correlation between predator presence and prey abundance.

Role of Social Organization

It is obvious that any factor which influences the numbers of individuals in an area will affect other structural aspects such as equitability, biomass, and spacing. Also, if differential mortality of various ontogenetic stages or sexes is induced by some environmental factor, the size structure and sex ratios of populations are affected. Such changes in one or more component species of an assemblage affects the structure of the entire assemblage. It is beyond the scope of the present paper to review the vast literature on the influence of the physical environment on population dynamics of herps. It is also beyond the scope of this review to assess in detail the role of biotic and social factors in such processes at the level of individual populations or species. However, certain features of social organization widespread in reptiles and amphibians that have an important bearing on assemblage structure will be summarized.

A recent symposium has made it evident that reptilian social behavior is extremely varied and that it plays an important role in the ecology and evolution of the group (American Society of Zoologists 1977). Aggression is a very common element in the social repertoire of many species of reptiles and amphibians and it finds its most common expression in territoriality (Carpenter 1967). Territoriality may involve only intraspecific aggression or may operate interspecifically. In the former, aggression may be only among adult males, among consexual adults, or take the form of adult attacks on juveniles. All of these forms of territoriality would tend to promote more uniform spacing and would limit the number of individuals that could occupy an area. This would in turn mean that successful defenders of territories in optimal habitat would have greater access to adequate food, mates, basking sites, and shelter than would less successful animals forced into marginal areas where chances of survival would be smaller. In fact, Done and Heatwole (1977*a*) suggested that aggression-based social systems result in a situation where, under unfavorable conditions or shortages, at least some individuals survive and breed rather than all die as a result of equally distributed but insufficient resources. Bradshaw (1971) showed that in *Amphibolurus ornatus*, adult aggression against juveniles forces the juveniles into areas where predation is higher; the surviving young migrate back into the adult areas when they reach sexual maturity. Thus, migration arising from a territorial social system may influence the structure of herpetofaunal assemblages in particular areas.

Interspecific territoriality may affect not only the number and spacing of individuals but of species as well. In some instances species occupy different horizontal or vertical zones depending on whether the area is shared or not with congeners (Jenssen 1973; Schoener 1975). It is also possible that species numbers may be affected by the exclusion from an area of a species by another interspecifically territorial one. Thus, territoriality may affect (1) spacing within a species, (2) spacing of species relative to other species, (3) numbers of individuals, or (4) number of species in an area. These factors in turn may affect equitability and biomass.

Not all species are territorial and some can shift from territorial to hierarchical systems, at least under the artificial conditions of captivity (Carpenter 1967; Hunsaker and Burrage 1969; Done and Heatwole 1977*a*, 1977*b*). The significance of different reptilian social systems to structuring in the assemblage has scarcely been assessed except for the effect territoriality in one species has on its own numbers and spacing, and on those of the species toward which it is territorial. One can, however, ask more synthetic questions. For example, can a given assemblage contain only so many territorial species? Are the proportions of territorial to non-territorial species subject to some degree of community regulation? Are species with a particular social organization replaceable by one with a different social behavior without altering the properties of the assemblage? These and other similar questions can only be answered by empirical comparative study of different assemblages. A move in that direction has been made by Williams and Rand (1977) who showed that the relative value of the dewlap and other communicative signals in anoles varies depending on the number of anole species in the assemblage.

Conclusions

All of the topics reviewed here relate to the form or structure that herpetofaunal assemblages take under different conditions. This is just one aspect of the study of assemblages, however. The complimentary topic to that of structure is function. To fully understand an assemblage or a community, not only must its structure be known but the flow of energy and materials among species must be assessed. Both these aspects are in their infancy as far as herpetofaunal assemblages are concerned. Bioenergetic studies on herps have usually been restricted to analysis at the single species level. It is hoped that this review, and this symposium, will stimulate herpetologists to devote increasing attention to studies involving the role of amphibians and reptiles in the structure and function of the larger community.

Acknowledgments

My ideas about the ecology of herpetofaunal assemblages have been influenced greatly over the years by stimulating interaction with colleagues on joint research projects. In this regard I am especially indebted to H. Cogger, R. Levins, J. Sexton, and to various of my Ph.D. students, particularly B. Firth, D. Horton, J. Parmenter, R. Shine, and G. Webb. The preparation of the manuscript was aided by A. Heatwole, R. Hobbs, N. Walden, and V. Watt.

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Amphibian Reproductive Ecology on the Community Level

by

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Abstract

A review of amphibian reproductive ecology emphasizes the lack of integration of life history strategies and community dynamics; no data are available on the influence of interspecific interactions in shaping reproductive strategies. Certain aspects of reproductive ecology within a community matrix are suggested for future investigation. Experimental field manipulations with appropriate controls and replicates will yield the most meaningful interpretation of interspecific interactions. A list of statements and predictions concerning amphibian reproductive ecology is presented, providing a framework upon which to ask relevant questions.

The concept of a community is an abstraction because of the dynamic and boundless nature of the system. Community in the broadest sense is the entire biotic component of an ecosystem, composed of all the interacting niche-differentiated species' populations. Logistics and practicality, however, require that ecologists delimit the boundaries of such a complex system for investigation. Thus, many ecologists adopt MacArthur's (1971) definition of a community as "any set of related organisms living near each other and about which it is interesting to talk." Community ecology is more than a composite of individual population studies; a major concern is species interactions. The scope, then, is determined by the investigator and the focus is on the intermeshing influences and responses exerted and elicited by the component species.

Recently there has been increasing interest in evolution at the level of communities. Levins (1975) suggested that selection acts differently on such variables as feeding efficiency, predator avoidance, and number of offspring on the community level as compared with the species level; selection at the community level does not necessarily favor each component species. He argued that there could be strong selection for perpetuation of groups whose component species have attributes that complement each other and that favor the persistence of groups through time. Wilson (1976) presented a model whereby selection can operate on the community level without violating the principle of Mendelian selection. It is not my intent here to enter the controversial argument on group selection, but rather to emphasize that populations do not exist in isolation from other populations.

Community organization is influenced by the simultaneous interactions of many species (MacArthur 1972; Pianka 1974; Colwell and Fuentes 1975; Whittaker 1975; Inger and Colwell 1977). Since species' responses are the result of coadaptations among sympatric populations, we must consider the organism within its entire environment to interpret adaptive strategies. Maiorana (1976*a*) also emphasized that a species' reproductive attributes and community ecology are interdependent and should be integrated fields of investigation. Species interactions are not simply pairwise; they are multidimensional, occurring between many if not most other populations in the community. Thus, in terms of the evolution and organization of the community, the whole is greater than the sum of its parts.

Using species interactions as the framework for community analysis, what do we know about amphibian reproductive ecology on the community versus the population level? Numerous autecological investigations have dealt with various aspects of amphibian reproductive ecology. These range from studies such as descriptive accounts of breeding periodicity, clutch size, and survivorship to long-term analyses of fluctuations in reproductive success and population age structure. A few studies have compared reproductive ecology of conspecific populations in different environments and others have compared populations of two sympatric species. However, whenever several sympatric species have been studied, the result is an interpretation of coexisting populations. The questions have not been cast into a community framework and species interactions have not been analyzed.

In reviewing the "state of the art" of amphibian reproductive ecology, I have been continually impressed by the lack of integration of amphibian life history strategies and community dynamics. Each species exhibits a particular set of reproductive adaptations in response to its entire environment, including the structure and stability of the community to which it belongs. Interpretation of the adaptive nature of reproductive factors should include examination of the relationships of these factors with those of coexisting species within the community framework. Just as community variables are important in molding reproductive patterns, the interwoven set of reproductive tactics exhibited by the component species in turn affects community structure and stability. Since each species' response may directly affect responses of other members of the community, the interactions of the component species produce synergistic effects on the overall community.

The review of amphibian reproductive ecology presented herein and the discussion of the mutual influences of community variables and reproductive patterns are meant to provide a framework for future investigation. The purpose of this paper, then, is threefold: (1) to review current knowledge of amphibian reproductive ecology; (2) to demonstrate the relevance of analysis of reproductive ecology on the community level; and (3) to suggest fruitful areas for further investigation.

Reproduction and Species Interactions

Like all artificially delimited communities, amphibian associations are continually changing in time and space. Many species of amphibians migrate from non-breeding areas to breeding sites (usually standing bodies of water) at appropriate times dependent on environmental conditions (see Salthe and Mecham 1974 for a review of environmental cues, breeding site location, and formation of breeding aggregations). The result at the breeding site is a different age-class distribution and sex ratio than that of the non-breeding population. In addition, species compositions at breeding sites differ from those at non-breeding sites. These compositional differences related to reproductive activity have effects on community structure, including fluctuating and overlapping resource utilization and species interactions. These effects have never been investigated. Predators of amphibians must also be affected by the transient associations with their continually changing compositions, but no data are available. Dispersal of juveniles away from the breeding site is probably the most important mechanism responsible for gene flow between populations; unfortunately, the effect of juvenile dispersal on overall community organization and stability has never been examined. The infusion of thousands of juveniles of numerous species into terrestrial habitats surely causes shifts in resource utilization among species; these shifts need to be quantified.

Although I could continue in this vein, perhaps it is more constructive to review the current status of our understanding of the mutual effects of reproductive ecology and species interactions. Two areas that have received considerable attention are reproductive isolating mechanisms and certain aspects of resource partitioning associated with breeding activity.

Reproductive Isolating Mechanisms

During the breeding season the potential for intraspecific and interspecific interactions is high because of the shift to a new community structure and a high density of individuals. Behavioral reproductive isolating mechanisms that help maintain species' identities are associated with the high potential for mismatings at temporary breeding congregations. These mechanisms include discriminatory courtship rituals such as species and sex recognition and mate selection. The most studied behavioral isolating mechanism in frogs is the mating call of males (for review see Salthe and Mecham 1974; Littlejohn 1977). The calls are species-specific with the frequency of the dominant harmonic, note repetition rate, and pulse rate and length relatively uniform within a species and variable among species. Male vocalization functions in orientation of both sexes to the breeding site, formation of breeding aggregations, sex discrimination, and location of specific males by females. Analyses of acoustical variables of mating calls from a community standpoint suggest that sympatric species exhibit significant call differences with only slight overlap (e.g., Blair 1956; Creusere and Whitford 1976).

Species recognition in salamanders is based on a complex of visual, olfactory, tactile, and behavioral cues (Salthe and Mecham 1974), the significance of particular cues varying from species to species; the complex courtship patterns in salamanders are probably significant in maintaining reproductive isolation (Arnold 1977). Behavioral interactions between rival males are well documented (Arnold 1976), but nothing is known concerning community interactions. If behavioral, visual, tactile, and olfactory cues could be quantified, they could be considered as "resource states" in a similar way that W. E. Duellman (personal communication) has analyzed community variables of frogs. A species' repertoire of reproductive isolating mechanisms probably has significant consequences to species interactions as well as to members of the opposite sex.

Resource Partitioning

Communities are organized, or have structure, as a consequence of interactions among the component populations; competition and predation are two types of interactions usually considered to be primary determinants of community organization. Predation represents interactions between trophic levels, whereas competition represents interaction within a trophic level. Although competition has generally been given greater consideration as a major determinant in amphibian community organization (e.g., Inger and Colwell 1977; Krzysik 1979), Hairston (1980) emphasized the potential importance of predation in *Desmognathus* community organization; he suggested that we need to design field experiments with testable hypotheses to partition out the organizing effects of predation versus competition. As Connell (1975) pointed out, however, these two determinants may themselves interact. Predation may reduce species densities such that competition is reduced or prevented.

Species interactions are expected to increase at temporary breeding sites because of the high density of individuals of many species. Community studies in the past have not taken into account shifts in resource utilization resulting from changing species composition. It would be of value to compare resource utilization of members of the non-breeding community with the same species in the breeding community. Analyses of spatial or temporal partitioning of available breeding sites (Crump 1974; Collins 1975; Creusere and Whitford 1976; Wiest, this volume) and partitioning of male calling sites (Littlejohn 1959; Bogert 1960; Duellman 1967; Dixon and Heyer 1968; Channing 1976) have generally suggested that these factors organize the community; the result is reduction of species interactions and increase in space partitioning, providing order in an otherwise potentially chaotic system.

On the other hand, my observations at Santa Cecilia, Ecuador, indicate that species composition of an anuran breeding aggregation may directly affect the partitioning of calling sites. Calling site specificity seemed to be less rigid when many species called sympatrically and synchronously. No differences in calling site were noted when individual species' densities were high as contrasted to an increase in number of species. One explanation is that some species may be flexible in their tolerance of acceptable calling sites. Perhaps species are not flexible at all; when displaced from preferred calling sites during periods of intense breeding activity, those males may not be successful in attracting mates. More work needs to be done on the effects of species composition and density on calling site partitioning and how displacements affect breeding success. If population fluctuations result from competition for optimal calling sites under conditions of high species-packing, community stability and resource partitioning would be affected significantly.

Oviposition sites constitute another spatial resource that is partitioned (Crump 1974). Of all the aquatic breeding assemblages studied in Ecuador, at the most 10 species of frogs were found depositing eggs sympatrically and synchronously. These species deposit their eggs in a wide variety of sites: free-floating on the water surface, wrapped around emergent vegetation stems in the water, on vegetation up to a meter above water, and suspended in a foam nest produced on the surface of the water. This environmental partitioning results in greater oviposition site use than if all 10 species required the same sites.

Foraging and shelter space as potentially limited resources for amphibians during the breeding period have not been investigated from a community standpoint. On the population level, many species have home ranges varying with sex, age, climatic conditions, and local geography. Sympatric species partition the environment, but whether this is indirect evidence of competition for space rather than the result of microhabitat preferences due to species differences such as in morphology, size, or physiological tolerance has not been investigated.

Food may be a major limiting resource for amphibians. One of the few studies comparing feeding habits during the breeding season with those during the non-breeding season indicated no difference in the percentage of individuals of two populations of *Pseudacris triseriata* which had food in their stomachs; about 65% of both populations had food in their stomachs (Whitaker 1971). However, significant qualitative differences were apparent. During the breeding season, vegetation and shed skin combined represented about 27% volume of stomach contents. During the non-breeding season, little vegetation was consumed (0.8%) and shed skins were not found in any stomachs. Whitaker found that *Hyla crucifer*, breeding sympatrically and synchronously with *P. triseriata*, does not feed at the breeding site. The combination of species-specific behavioral differences plus the fact that different prey items would be expected to be found in terrestrial versus aquatic sites suggest that shifting food utilization is probably extremely important to overall community organization.

When analyzing species interactions within an amphibian community, one must be aware that the system is dynamic, and species associations are constantly changing (Goin and Goin 1953; Wiest, this volume). Information for a species-pair combinations in one time frame should not be extrapolated to another life history stage. Ecologists often interpret the activities of members of a community as means of "avoiding" competition. Species differences are often labeled as "mechanisms" permitting coexistence. As pointed out by Peters (1976) and Wiens (1977), however, the concept of competition is a tautology rather than a testable theory. Nonetheless, investigators can and should obtain quantitative measurements on available resources and determine differential utilization levels.

Mode of Reproduction, Species Richness, and Resource Partitioning

Often an obvious reproductive difference between species is the mode of reproduction, referring to a combination of egg deposition site and mode of development (including whether development is larval or direct, size and stage at hatching, and rate of development). Associated with mode of development is a wide variety of clutch sizes and egg sizes. Numerous authors have discussed evolutionary trends in amphibian reproductive modes and life history patterns (Noble 1927; Lutz 1947, 1948; Orton 1951; Jameson 1955, 1957; Goin 1960; Lynn 1961; Goin and Goin 1962; Tihen 1965; Heyer 1969). The commonly proposed trend is evolution towards greater terrestrialism. In this section several questions will be addressed: (1) How much variability is there in mode of reproduction within frogs and salamanders? (2) How is clutch energy partitioning related to reproductive mode? (3) Is there a relation between diversity of reproductive modes and species richness? and (4) Does reproductive mode diversity affect partitioning of space resources?

Salthe (1969) categorized salamanders into three modes of reproduction: (1) Eggs are abandoned in open, still water; the eggs are relatively small, and hatch at comparatively early stages of development. (2) Eggs are deposited beneath objects (such as rocks) in running water; the eggs are larger than those of mode 1, the larvae hatch at a more advanced stage, and many species exhibit parental care by guarding the clutch until hatching. (3) Eggs are deposited in one mass, beneath objects on land; the eggs are larger than those of the other modes, clutch size is smaller, development is direct, and parental care is present in most species.

Anuran species with a generalized reproductive mode deposit eggs directly in water and have an aquatic larval developmental stage (modes of reproduction collectively referred to here as

Group I; from Crump 1974). Less generalized are species that deposit eggs out of water but retain an aquatic larval stage (Group II). The most specialized forms are totally independent of standing water (Group III). Some Group III species deposit terrestrial eggs that undergo direct development; in other species, development takes place within the body of the adult, within a foam nest, or in some other protective situation. Parental care is present in some species.

Quantitative variables of clutch size associated with mode of reproduction influence the genetic variability maintained by a population. The optimal balance between clutch size and egg size, or the partitioning of clutch energy, ultimately is a function of the levels of competition, predation, and environmental uncertainty to which the young are exposed (Smith and Fretwell 1974; Brockelman 1975; Wilbur 1977*c*). Empirical interpretations of the relation between egg size and clutch size for amphibians are provided by Salthe (1969), Salthe and Duellman (1973), Crump (1974), Kuramoto (1978), Kaplan and Salthe (1979), and Crump and Kaplan (1979). Generalized species (Group I) characteristically have large clutch sizes relative to female body size. The eggs are small and intraoval development is rapid; the resultant hatchlings are small and are at a comparatively early stage of development. These species tend to breed in the most unpredictable environments, such as temporary ponds and ditches. Species of more specialized modes of reproduction (Groups II and III) produce fewer but larger eggs relative to body size; many of these species have direct development. Groups II and III species breed in the most stable environments such as under leaf litter on the forest floor or in rotting logs; they may exhibit some form of parental care. Presumably Group I species, with larger clutch sizes, maintain higher genetic variability within local demes than do species having more specialized modes of reproduction.

One of the most notable differences in life history features of temperate versus tropical anuran communities is the increased diversity of reproductive modes in the tropics. In areas of greatest species richness there is concomitant high diversity of reproductive modes (Salthe and Duellman 1973; Crump 1974). The evolution of diverse reproductive modes in the New World tropics may have occurred in response to competition for limited breeding sites, as a response to predation pressure on aquatic eggs, as a means of avoiding desiccation problems in ephemeral aquatic environments, as a result of larval competition for food, or any combination of these factors.

Differences in diversity of reproductive modes have been invoked to explain the considerably greater species richness in tree buttress microhabitats in Ecuador (21 species of frogs at the study site) as compared with similar microhabitat in Thailand (1 species, Heyer and Berven 1973). Four of the Ecuadorian species deposit terrestrial eggs and then transport the larvae to water; eight species deposit terrestrial eggs that have direct development and are therefore completely independent of standing water. In Thailand, the only frog in the buttress microhabitat is a microhylid that breeds in standing water. The greater species richness of lowland litter anuran communities in Costa Rica as compared with Borneo and Cameroon has also been attributed to the exploitation of the terrestrial environment in the New World tropics by direct-developing species (Scott 1976, this volume). The mode of terrestrial eggs and direct development seems to be an extremely successful strategy for avoiding stressful environmental uncertainties and fluctuations in tropical areas. It is significant that whereas all of the common leaf litter frogs in Borneo depend upon standing water for larval development, a high proportion of the fauna at various sites in Costa Rica are totally independent of aquatic sites.

Crump (1974) analyzed spatial resource partitioning of anuran breeding communities from the standpoint of modes of reproduction. In an area of 3 km^2, the 78 sympatric species were categorized as follows: 36 species of Group I, 25 species of Group II, and 17 species of Group III. Most of the 61 species dependent upon standing water for breeding purposes demonstrated restricted utilization of the aquatic sites. Some species preferred open, disturbed areas, whereas others were found only at ponds in mature forest; no species was distributed regularly within the habitats. Temporal differences in breeding activities were also a major segregating factor for species breeding at one site. Partitioning of the available oviposition sites was largely a function of requirements dependent on the particular mode of reproduction. Data on spatial and temporal utilization of breeding sites suggested that the reproductive diversity at Santa Cecilia is a major factor contributing to the coexistence of the most species-rich fauna yet studied.

There have been no studies relating reproductive modes of salamanders to community ecology. However, we may predict that in communities characterized by a large diversity of modes of reproduction, increased spatial resource partitioning may be associated with fewer interspecific interactions and greater species richness, the same as it is for frog communities.

Population Variability in Life History Patterns

Considerable theory concerning contrasting life history patterns and the mechanisms leading to their evolution has been presented (see Giesel 1976; Pianka 1976; Stearns 1976, 1977; for literature reviews and syntheses of these ideas). Major factors influencing reproductive patterns are local climatic conditions and the relations between the density of a species and the availability and abundance of its resources (MacArthur and Wilson 1967; Pianka 1970). Wilbur et al. (1974) included predictability of mortality patterns as an important determinant of adaptive strategies. Habitat certainty is also important to amphibian life histories (Low 1976). Wilbur et al. (1974) and Maiorana (1976*a*) emphasized that since evolutionary processes result from synergistic effects, a number of factors influencing life history patterns should be considered simultaneously.

Although we have begun to interpret life history patterns on the population level, the community approach to life history patterns is at a primitive stage of development and few such studies exist. Crump (1974) and Collins (1975) discussed differences in many life history variables of anuran species within two communities. Due to the extreme difficulty in dealing with species-rich aggregations, however, the life history patterns were analyzed from a population standpoint in both studies.

A community analysis of life history patterns would provide insight as to how populations are co-adapted, or how the patterns of one species affect another's strategy. Because no such data are available, the following is a review of variability in life history patterns on the population level. These generalizations should provide a framework upon which to ask relevant questions regarding life history patterns on the community level.

Environmental Influence on Life History Patterns

A species may be thought of as a mosaic of populations, each adapted to local environmental conditions and therefore divergent in life history features (Ehrlich and Raven 1969). Rainfall, water temperature, and permanence of the aquatic breeding site exert significant influences on yearly variation in timing of reproduction and length of the larval period. Geographically separated populations of amphibians may differ in egg size, developmental rates, clutch size, age at first reproduction, and breeding periodicity, depending on environmental factors.

Geographical differences in life history features may be related to decreased activity periods of northern populations. Increasing evidence reveals biennial breeding cycles of northern populations and annual cycles for southern populations of plethodontid salamanders (Highton 1962; Sayler 1966; Hall and Stafford 1972; Nagel 1977). Some evidence suggests slower growth rates and delayed maturity in northern individuals; the higher fecundity resulting from increased body size in northern individuals perhaps compensates for the biennial breeding cycle (Highton 1962).

Altitudinal comparison of populations also reveals contrasting life history patterns. Female *Rana temporaria* are larger in mountain populations and deposit fewer but larger eggs than females in lowland populations; weight of the clutch relative to female body weight is lower in highland females, suggesting a smaller reproductive effort per breeding period (Kozlowska 1971). Berven et al. (1979) studied life history features of *Rana clamitans* along an altitudinal gradient. Transplantation experiments and laboratory studies suggest that variation in certain life history features can be environmentally induced by temperature effects alone. When grown under identical low temperatures, high-elevation larvae grew faster and completed metamorphosis earlier and at a smaller size than lowland individuals; this suggests that selection along the altitudinal gradient has minimized the effects of environmental variation and has favored the most rapid larval development possible within temperature constraints. These results agree with studies by Moore (1939) that demonstrated that cold-adapted species show faster embryonic rates of development at any given non-lethal temperature than warm-adapted species.

Influence of Age-Specific Mortality Predictability and Stable Environments on Life History Patterns

A major determinant of life history adaptations is the certainty of the environment relative to each life history stage. Amphibians demonstrate contrasting reproductive responses in unchanging environments versus fluctuating environments. Low (1976) emphasized the importance of environmental uncertainty on anuran life history strategies and pointed out that an effect of metamorphosis is an increase in independence of variation in survivorship in different life stages; in uncertain larval environments, a premium is placed on strategies that enable facultative breeding responses and reduce the chance of total reproductive failure. In unchanging environments, late maturity, multiple clutches, fewer but larger eggs, parental care, and small reproductive efforts should be favored; in fluctuating environments the reverse correlates should appear (MacArthur and Wilson 1967; Hairston et al. 1970; Pianka 1970). However, as Schaffer (1974) pointed out, life history patterns should vary depending on age-specific mortality. If the environment of the juvenile stages is uncertain, leading to high or unpredictable mortality, different strategies should be selected for as contrasted to those in environments that are uncertain for adults, leading to high or unpredictable mortality at that stage (Low 1976).

Differences in egg deposition patterns, fecundity, and parental investment of several sympatric species of *Ambystoma* are best interpreted as adaptations to adult survival and to the degree of certainty of the larval environment (Wilbur 1977*c*). Of the species compared, *Ambystoma laterale* breeds in the most temporary environments; this species expends the highest reproductive effort relative to body size and seemingly has sacrificed egg size for increased clutch size. Small eggs are deposited singly and hatch into larvae that develop rapidly; the ability of these larvae to metamorphose over a wide range of body sizes is considered an adaptation to unpredictable environments. *Ambystoma tigrinum*, which breeds mostly in permanent ponds, deposits its eggs in several clumps. Although larval survivorship is relatively constant from year to year, adult survivorship is low. For this reason, high reproductive output by the female is favored, as demonstrated by early maturity and high fecundity. *Ambystoma maculatum* deposits eggs in a single mass in semipermanent ponds. Because larval survivorship is variable and adult survival is high, it is advantageous for a female to reproduce as many times as possible. By expending a low reproductive effort each year, females can reproduce more total times per lifetime to compensate for uncertain juvenile survivorship.

Danstedt (1975) studied life history characteristics of six populations of *Desmognathus fuscus* in four physiographic provinces in Maryland. Although many factors were similar in these populations, ovarian egg complement differed significantly; females from populations where adult survival was lower produced significantly more eggs. Part of the explanation is that body sizes were larger, and there is a positive size-fecundity relation. However, these females also produced more eggs per unit body size. Since egg size does not vary geographically, apparently females expend proportionately greater amounts of energy on reproduction in those populations where adult survival is lower.

Theorists predict that reduction of age at first reproduction results in a large gain in the intrinsic rate of natural increase (r; Cole, 1954; Lewontin 1965). Early reproduction usually is indicative of fluctuating juvenile survivorship, uncertain breeding conditions, or fluctuating population densities. Several amphibian studies provide empirical support for this prediction. In Massachusetts coastal populations of *Notophthalmus viridescens* inhabiting harsh and unstable environments, selection favors a high r; the terrestrial eft stage is omitted and individuals begin reproducing at age 2 (Healy 1974). Inland populations retain the eft stage and range from 4 to 8 years old at sexual maturity. In the more stable inland environments, individuals apparently are not under selection for a high r. Likewise, populations of *Desmognathus ochrophaeus* in contrasting environments of North Carolina differ with respect to age at maturity (Tilley 1973*a*, 1973*b*). Delayed reproductive maturity in high-elevation woodland individuals is accompanied by a larger body size and concomitant increased age-specific fecundities; unstable age structure exhibited by a low elevation woodland population suggests greater density fluctuations. Differences in life history features of populations of *Rana pretiosa* from low and high elevations support the hypothesis that earlier age at maturity should be selected for in environments of periodic reproductive failure (Licht 1975). In the lowland area the entire reproductive effort may be lost in any given year due to drought. A markedly slower growth rate and delayed sexual maturity were evident in the high-elevation population. Clutch size was the same, but lowland females bred annually, whereas high-elevation females bred only every 2 to 3 years. Further support for the hypothesis is provided in comparative studies of *Gyrinophilus porphyriticus*. Selection has favored earlier maturity and higher size-specific fecundity in low-elevation individuals, as contrasted to high-elevation individuals (Bruce 1972). The low-elevation habitats are smaller, more isolated, and seem to be subjected to greater climatic fluctuation. These factors would increase chances of local extinction, favoring selection of life history features characteristic of colonizing species.

Individuals living in fluctuating environments should exhibit flexibility in life history features. Bruce (1975) suggested that the irregular breeding cycle of female *Pseudotriton montanus* in the Piedmont of western South Carolina is an adaptation that both favors longevity and provides for iteroparity (reproducing more than once in a lifetime) and yet allows for high fecundity. Individuals of *Batrachoceps attenuatus* in an area of California that experiences a variable, prolonged dry season, are also extremely flexible in their life history characteristics; they are able to maximize reproductive effort per lifetime even though the environment favors both longevity and high fecundity (Maiorana 1976*b*). Since individuals have an uncertain life expectancy (because of high predation and an unpredictable climate), selection favors a high reproductive output when energy is available.

Thus, empirical studies support the prediction for contrasting strategies in response to certainty of survivorship and habitat. The following correlate of this prediction is testable: In circumstances where larval survivorship varies unpredictably in time, smaller clutch sizes should be favored because they decrease the chances of total failure for any given breeding period. In such instances, selection favors the strategy of small numbers of young being produced at staggered times throughout the year rather than the strategy of synchronous development of a larger number of offspring (Pearson 1960; Murphy 1968; Schaffer 1974). An alternative to spreading reproductive effort throughout time is deposition of partial clutches throughout space (Salthe 1969; Wilbur 1977*c*).

In virtually all amphibian populations studied, predation on young is high and juvenile mortality fluctuates more than does adult mortality. Thus, we would expect the above correlation with smaller clutch size to be true for amphibians. However, reproductive success of most amphibians is closely coupled to appropriate environmental conditions. In the temperate zone, largely because of seasonal restrictions, the breeding pattern is a rather synchronized recruitment of young into the population at widely spaced intervals; most individuals breed only once per year. An exception, however, is certain ranids that produce two clutches per year (Wells 1976; Emlen 1977). On the other hand, in climates amenable to year-round reproductive activity, the pattern seems to be continued reproduction at least by the population (Inger and Greenberg 1963; Berry 1964; Valdivieso and Tamsitt 1965; Inger and Bacon 1968; Vial 1968; Anderson and Worthington 1971; Crump 1974; Duellman 1978). Most of these studies present indirect evidence of multiple breeding per individual per year; examination of ovaries of females that have recently oviposited reveals at least one additional size class of eggs soon to be matured.

Inger and Greenberg (1966*a*) discussed the implications of noncyclic reproductive patterns in a nonseasonal environment. Species for which breeding activity is cyclic (characteristic of seasonal environments in both temperate and tropical areas) would be affected in a pulsating manner; the infusion of juveniles at only certain intervals might result in potential competitive interactions for limited resources. The cyclic nature would also affect the remainder of the biotic community as the young would provide only a temporary food source for predators. Noncyclic reproductive patterns are typical of many nonseasonal areas where little-fluctuating environmental conditions permit continual breeding, creating a situation of overlapping generations. Inger and Greenberg (1966*a*) suggested that year-round reproduction probably buffers population fluctuations and therefore may be a major factor contributing to the high species diversity of the nonseasonal tropics. Duellman (1978) supported this hypothesis in his analysis of the herpetofaunal community at Santa Cecilia, Ecuador, and pointed out that there would be greater genetic mixing in nonseasonal habitats associated with increased matings per unit time as compared with seasonal environments.

Scattering of the eggs in space potentially increases survivorship. Many species of amphibians deposit eggs either singly or in multiple masses distributed in the habitat. On the other hand, parental care has evolved in association with deposition of a single mass of eggs, presumably as a means of increasing embryonic survivorship. A system of repeated matings by a female with different males throughout time decreases the possibility of total reproductive failure and simultaneously increases genetic variability within the population (e.g., Crump 1972; Woodruff 1976*a*).

Population Demographic Considerations and Community Stability

In considering population regulation, the following questions are frequently asked: (1) What is the reproductive potential of the population? (2) What is the realized reproductive performance of the population? (3) What is the environmental resistance (reproductive potential minus the realized performance of the population)? (4) How do age-specific fecundity and mortality vary in time and space? (5) What is the population turnover rate? and (6) What is the relative importance of density-dependent versus density-independent regulating factors?

Community stability is influenced not only by fluctuations of the constituent populations, but by the interactions and joint influences of coexisting species. One cannot examine community variables by dissecting out the component populations; the interactions between the species must be analyzed. No such studies have been carried out on entire amphibian communities. In fact, Turner (1962) noted that there have been few demographic analyses of anuran populations, as data on natality, mortality, and age-class distribution are extremely difficult to collect; the same is true for salamander populations. A major problem is the lack of a suitable technique for aging the animals in the field (Cagle 1956).

The size of the breeding population has considerable effect on the evolutionary processes and population dynamics (Wright 1969). The effective breeding population of most amphibians is usually much less than the total population; generally males are many times more abundant than females in the breeding community (Blair 1943; Martof 1956; Husting 1965; Merrell 1968; Morris and Tanner 1969; Whitaker 1971; Hedeen 1972; Calef 1973*b*). Unfortunately, no data are available on the implications of this phenomenon to community structure.

There are few quantitative estimates of embryonic mortality in nature, but evidence suggests that mortality is low except in the event of environmental catastrophe (Woodruff 1976*b*). Age-specific mortality is highest in the larval stage of the amphibian life cycle (Savage 1952; Turner 1962; Moore 1963; Herreid and Kinney 1966; Licht 1968; Anderson et al. 1971; Calef 1973*a*; Heyer 1976) and varies widely among breeding sites in one area, geographical areas, species, and years (Pearson 1955; Martof 1956; Turner 1960; Brockelman 1969; Scott and Starrett 1974; Shoop 1974; Walters 1975); survivorship to metamorphosis often varies between 0 and 10%. For this reason, larval mortality plays a central role in regulating population size. Larval communities in temporary aquatic sites are usually characterized by highly fluctuating population sizes. The low survivorship of larvae is usually related to high predation or severe catastrophic phenomena such as evaporation of the aquatic breeding site. Walters (1975) suggested that synchronized breeding by certain palatable species of amphibians may increase survival through predator satiation. Brockelman (1969) found that high predation rates may actually benefit individual larvae by eliminating negative effects on growth by reducing crowding effects.

Experimental field and laboratory studies have shown that the proportion of a larval population that survives to metamorphosis and the mean body size at metamorphosis are inversely related to population density; in high-density experimental populations, a small number of individuals grow and metamorphose at the expense of the remainder of the cohort (Brockelman 1969; Wilbur 1972, 1976, 1977*a*, 1977*b*; Wilbur and Collins 1973; DeBenedictis 1974). The rate at which larvae feed and metamorphose is of critical importance not only in the potentially competitive and predator-rich aquatic environment (Worthington 1968; Wilbur and Collins 1973), but also from the standpoint of the ephemeral nature of many breeding sites (Shoop 1974).

The adaptive significance of the larval stage lies in the use of abundant, but ephemeral, resources in the aquatic environment; the temporal nature of these resources is significant as it assures a time lag in the buildup of predator populations (Wassersug 1975). Amphibian larvae grow rapidly and fit a sigmoid growth model; there is considerable variability in growth rates within a population leading to a skewed distribution of body size at metamorphosis such that there are many more small individuals than large (Wilbur and Collins 1973). Species that exploit uncertain environments generally have a wider range of possible developmental times and sizes at metamorphosis than species that breed in relatively certain habitats. Some investigators conclude that food is not a limited resource in larval communities and that larval populations and communities are largely regulated by predators (Calef 1973*a*; Heyer 1973, 1974, 1976; Heyer et al. 1975), whereas others present data suggesting that food is limiting and serves as a density-dependent regulating factor (Savage 1952; Brockelman 1969; Wilbur and Collins 1973; DeBenedictis 1974; Wilbur 1976, 1977*a*, 1977*b*).

Anurans are particularly susceptible to snake predation during the metamorphic transition because they can neither swim as effectively as premetamorphic tadpoles nor hop as effectively as postmetamorphic frogs (Wassersug and Sperry 1977). Considering the drastic changes that take place during metamorphosis, anurans spend disproportionately little time in this stage. Wassersug and Sperry (1977) pointed out that the rapidity of transformation minimizes the amount of time spent in this vulnerable stage. In many species (e.g., *Bufo* and *Scaphiopus*), numerous individuals metamorphose in synchrony; Arnold and Wassersug (1978) suggested that metamorphic synchrony may have evolved as a mechanism for satiating predators.

Very little is known concerning juvenile survivorship between the time individuals disperse from the breeding site and their return to a breeding site when reproductively mature. Bannikov (1950) estimated mortality in *Bombina bombina* between metamorphosis and 1 year to be about 98%; mortality during the next year was about 40%, and during the third year, almost 100%. On the other hand, Green (1957) estimated postmetamorphic age-specific mortality at a constant 70% for a West Virginia population of *Pseudacris brachyphona*. Likewise, Turner (1960) found no significant age-specific survivorship differences among age classes of a population of *Rana pretiosa*. Studies of certain species of *Rana* in the tropics indicate relatively stable postmetamorphic age structures within populations (Alcala 1955; Inger and Greenberg 1963, 1966*b*; Brown and Alcala 1970). Husting (1965) found that survivorship was higher for male *Ambystoma maculatum* than for females, and Organ (1961) found the same for species of *Desmognathus*; on the other hand, Bell (1977) found a lower survivorship for male *Triturus vulgaris* than for females.

Common newts (*Triturus vulgaris*) demonstrate considerable variability in life history patterns, passing through or eliminating several distinct ecological niches depending upon when in the season they metamorphose and whether they mature early or late (Bell 1977). Bell suggested that this complexity might have two effects on the population: increase in the level of genetic variability and reduction in fluctuation of population size since a disaster in one niche would not result in extinction of the entire population. In the common newt it is clear that population age structure has significant consequence to resource utilization; however, this is probably a widespread phenomenon among amphibians since there is considerable variability in age and size at metamorphosis. The effects of demography on the community level are probably of great significance to community organization and stability.

Turner (1962) suggested that if we assume that differences in metabolic rate result in different life-spans, then life expectancy should be longer in seasonal, temperate areas where growing seasons are shorter and temperatures lower than in nonseasonal tropical areas. Nonseasonal tropical communties would then be expected to consist of populations with high turnover rates. Data on a shorter life-span for *Rana erythraea* relative to temperate ranids support Turner's hypothesis (Brown and Alcala 1970). This comparison can also be viewed from a life history standpoint. Since it appears that individuals in nonseasonal regions produce smaller clutches at more frequent intervals than their counterparts in seasonal environments, a shorter life-span would be expected in nonseasonal environments based on energy budget considerations. The "live fast and die young" cliché suggests that individuals that allocate large energy investment to reproduction rather than to somatic functions would be expected to die sooner. This prediction supports the correlate of the *r*- and *K*-selection model that associates high productivity with a short life-span (Pianka 1970), and leads to the same conclusion: nonseasonal environments should be associated with populations with higher turnover rates. How population turnover times and fluctuations affect overall community structure and stability provides a stimulating question for future ecological research. As emphasized earlier, no data are available on the extent to which sympatric amphibians influence the demography and population stability of each other nor how they affect overall community stability.

Conclusions

Although there has been a considerable number of population studies concerning the reproductive ecology of amphibians, there has been little integration of reproductive ecology and community dynamics. Because amphibians have shifting community structures and compositions, integration of these aspects is challenging. I have discussed various ways in which community structure, species interactions, community stability, and reproductive attributes of species are interdependent. Major reproductive aspects that should be related to community dynamics include (1) reproductive isolating mechanisms, (2) resource partitioning associated with breeding activity, (3) activity such as migration of adults to breeding sites and dispersal of juveniles from breeding sites, and (4) life history patterns including mode of reproduction, clutch size, iteroparity, age at first reproduction, and demographic variables.

Reproductive isolating mechanisms and resource partitioning at breeding sites are important concepts at the population level, but few studies have analyzed them from the community standpoint. Mode of reproduction has significant implications for species diversity and resource utilization: the greater the reproductive diversity the more species can coexist, perhaps because of greater resource partitioning. The spacing of recruitment of young into the population and how this relates to the overall community in terms of the patterns of coexisting species is of significance to resource utilization, species interactions, predator–prey relations, demography, and therefore ultimately to community organization and stability. Investigators are beginning to understand variability in age-specific fecundity and survivorship, age at first reproduction, age-class distribution, sex ratios, and longevity within populations. However, because natural selection favors individuals that are most successful in the overall environment (in addition to intraspecific interactions), one must integrate reproductive attributes with overall community ecology to interpret an animal's adaptations.

Using the information from the studies discussed as a base line, I submit that analysis of life history patterns on a community level is a feasible endeavor. The study of the relation between life history variability and community organization, species interactions, and community stability presents a challenging field of research. In attempting to integrate reproductive attributes and community ecology, specific questions must be asked. For practical reasons, one should begin with a relatively simple community consisting of only a few species of amphibians. Laboratory experimental studies could provide preliminary data on species interactions and influences, but eventually one would want to study a natural community. Carefully designed and executed field manipulations are essential to interpret adaptive strategies on the community level (see Connell 1975; Stearns 1976; Wiens 1977; Hairston 1980).

The following statements and predictions provide a framework upon which to ask relevant questions:

- Migration of amphibians to aquatic breeding sites and dispersal of juveniles away from sites result in different community compositions, affecting many aspects of community organization.
- Species of anurans breeding sympatrically or synchronously exhibit only slight (if any) overlap in acoustical variables of mating calls; many species have characteristic calling sites, resulting in an increase in use of spatial resources and enhancement of species recognition.
- Breeding sites within a given area are generally partitioned in time and space, resulting in greater use of the available sites and reduced species interactions.
- Species-specific requirements of oviposition sites differ such that within any mixed-species breeding aggregation there is increased utiliza-

tion of space, resulting in a greater species-packing than possible otherwise.

- Overlap in food utilization at breeding sites may be reduced by species-specific behavioral and preference differences.
- There is a postive relation between species richness and diversity in modes of reproduction; the tropics are the highest in both.
- Generalized amphibians (those that abandon eggs in open water) have larger clutch sizes relative to body size than do more specialized species (those that deposit eggs on land, often exhibiting some form of parental care). The higher fecundity of generalized species possibly results in increased variability maintained by the populations; these species usually breed in more temporary or fluctuating sites than do more specialized species, which generally deposit larger eggs with increased energy investment per offspring in more stable environments.
- Partitioning of breeding and oviposition sites related to high diversity of modes of reproduction in the tropics is a major factor contributing to the existence of species-rich communities.
- Life history patterns are in large part molded by local climatic conditions, resource availability, habitat certainty, and predictability of age-specific mortality.
- Many species exhibit latitudinal differences in various life history variables (e.g., biennial breeding cycles in northern populations versus annual cycles in southern populations). Delayed maturity, resulting in larger body sizes and therefore higher fecundity, perhaps compensates for the biennial breeding cycles of northern individuals.
- Unpredictable or otherwise harsh environments resulting in low adult survivorship favor early reproductive maturity, flexibility in life history features, and high fecundity. When adult survival is high, it is advantageous to increase iteroparity; by expending a low reproductive effort per clutch, individuals can breed more often per unit time.
- Unpredictable or otherwise harsh environments resulting in low or unpredictable larval survivorship favor either increased iteroparity with small clutches per breeding period or deposition of partial clutches scattered in space.
- Noncyclic breeding patterns (typical of nonseasonal areas) result in overlapping generations and probably buffer population fluctuations. Genetic mixing is probably increased from the increased matings per unit time. Year-round reproduction may be a major factor contributing to high species diversity in the nonseasonal tropics.
- Larval mortality plays a central role in regulating population size. Age-specific mortality is highest during the larval stage of the amphibian life cycle and fluctuates considerably between breeding sites and from year to year.
- There is considerable variation in larval growth rates within populations leading to a skewed distribution of body sizes at metamorphosis. Species that breed in relatively certain environments exhibit a narrower range of developmental time and body size at metamorphosis than do species that exploit uncertain habitats. The proportion of a larval population that survives to metamorphosis and the mean body size at metamorphosis are inversely related to the larval population density.
- Amphibian communities in nonseasonal tropical regions are expected to be composed of individuals that have shorter life-spans than comparable species in seasonal temperate zone areas. This would result in populations with higher turnover rates, which would ultimately affect overall community organization and stability.

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AMPHIBIAN COMMUNITIES

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Anuran Succession at Temporary Ponds in a Post Oak–Savanna Region of Texas

by

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Abstract

Reproductive patterns of anurans using temporary ponds in a Texas post oak (*Quercus stellata*) savanna region were studied during an abnormally wet year, September 1972 through September 1973. Anuran succession was correlated with varying environmental conditions. The overriding causes of variation in anuran reproductive patterns were fluctuations in air and water temperatures, rainfall, and possibly humidity.

Calling, breeding, and larval periods for nine species are discussed. The vocalization sequence, based on the first evening when calling was heard for each species, was as follows: *Pseudacris streckeri*, *P. triseriata*, *Scaphiopus holbrooki*, *Acris crepitans*, *Hyla versicolor*, *Bufo valliceps*, and *Gastrophryne olivacea*. Exceptions to this sequence were *Rana sphenocephala*, which called in practically every month of the year, and *P. clarki*, which had a primary calling period in the winter-spring months and a short opportunistic calling period in late summer. *Bufo speciosus* and *B. woodhousei* were uncommon and their status in the study area is discussed. For most anurans there was a larval bloom in April and May, which were the months with the most rainfall.

The reproductive habits of the anurans of the United States are sufficiently well known to indicate that some general patterns exist in the timing of anuran reproductive activities. However, varying environmental conditions may drastically alter the time and length of the breeding season. Information is still lacking concerning the reproductive cycle of one species relative to other anuran species at any given locality. Successional studies of various durations have been reported for a few specific localities in the United States (Goin and Goin 1953; Blair 1961; Murphy 1963; Rubin 1968) and in other countries (Frazer 1956; Neal 1956; Berry 1964; Dixon and Heyer 1968; Inger 1968; Heyer 1973).

The objectives of the present study were to investigate anuran succession at temporary ponds in a post oak (*Quercus stellata*) savanna region of Brazos County, Texas, and to determine the effects of certain environmental factors on the reproductive season of anuran species observed. The few previous anuran succession studies have been conducted in widely separated localities, and therefore more successional studies are needed before patterns of anuran reproductive activity can be properly synthesized. The particular importance of this study is that it includes observations of both adults and larvae in establishing a localized pattern of anuran succession.

Description of Study Area

Brazos County, in east-central Texas, is bordered by the Brazos River on the west and by the Navasota River on the east. This county is in the Texas Province, a broad ecotone between the forests of the Austroriparian province of eastern Texas and the grasslands in western Texas (Dice 1943; Blair 1950). The area is considered a post oak savanna region (Gould 1969), except for a small northern portion designated as blackland prairie. Typical of the post oak belt, the county has an elevation of 61 to 122 m; the surface slopes toward the southeast. The topography is level to gently rolling with no conspicuous relief.

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Materials and Methods

Anuran succession was followed from 3 September 1972 to 28 September 1973. The study included most Brazos County anuran species that use temporary ponds for breeding. Calling dates for males were noted, as were reproductive activities such as amplexus or egg deposition. All data were collected at temporary ponds, herein defined as bodies of water which usually become dry during some portion of the year. Five temporary ponds served as the primary study areas and seven others were observed at various times throughout the study. Wiest (1974) provided a detailed description of each pond site including exact location, surrounding terrain, dimensions, depth, water clearness, periods of dryness, and vegetation in and around the ponds. Before 30 June 1973, observations of adult breeding behavior were conducted nightly, and larvae were collected every 3–4 days. Beginning 1 July 1973, night observations were made only after periods of rainfall, and larval collections were made every 2 weeks. Adult habitat, duration of day-night activity, calling sites, breeding sites, larval habitat and larval feeding, and aggregational behavior were recorded.

Larvae were collected during afternoons with a dip net. Quantitative sweeps were not taken, but rather attempts were made to sample different microhabitats and all distinctive larvae. Usually less than 10 individuals of each species were retained at each site on a given date. Air temperatures at 1 m and 2.5 cm above ground and water temperatures at depths of 2.5 and 10 cm were recorded with each afternoon larval collection. All larvae were staged according to Gosner (1960).

Environmental data were collected during evening observations to determine the effects of the environment on reproductive seasons. Air temperatures at 1 m and 2.5 cm above ground, at ground level, and the water temperature at a depth of 2.5 cm were recorded at each pond nightly. A sling psychrometer was used to determine relative humidities during evening observations. Daily maximum and minimum temperatures, daily mean wind velocity, daily wind velocity and direction between 1900 and 2300 h, and daily rainfall were obtained, in part, from Easterwood Airport Weather Station, College Station; the Texas A&M University Weather Station, College Station; and from James R. Dixon's residence at 705 Inwood Drive, Bryan, Texas. Rainfall was recorded in millimeters and noted as to time and duration.

Climatological Considerations

The climate of Brazos County is relatively mild. From May through September, prevailing southeasterly winds from the Gulf of Mexico produce high humidities and limited temperature changes. From November through March, northerly winds become prevalent and are often accompanied by sudden temperature changes which result from the interaction of polar and tropical air masses. Cold spells are most severe and frequent from December through February. April and October are transitional months. The mean annual temperature is 18.3°C, and the maximum and minimum recorded temperatures are 43.3° and −19.4°C. The average annual precipitation is 984 mm; heaviest rainfall occurs from April through June. Droughts are common during summer months. Snow is rare and seldom accumulates. Annual relative humidity is about 70% and monthly variations are small.

Weather conditions for 8 months preceding the start of this study were normal, except rainfall was below monthly averages (Fig. 1). Weather data obtained in the field were compared with the mean monthly temperatures and rainfall data for 1933 to 1973 (taken from Climatological

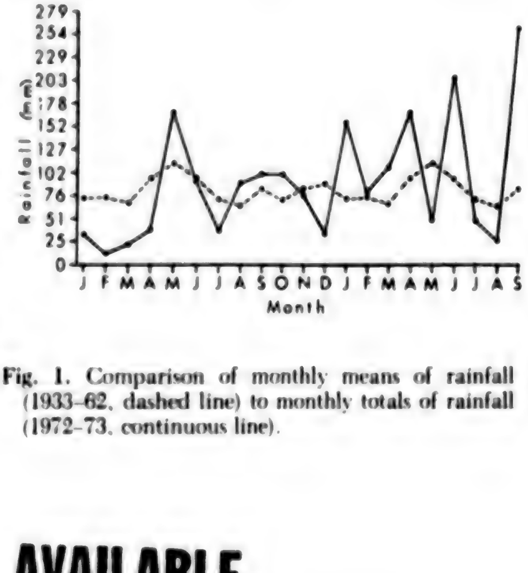

Fig. 1. Comparison of monthly means of rainfall (1933–62, dashed line) to monthly totals of rainfall (1972–73, continuous line).

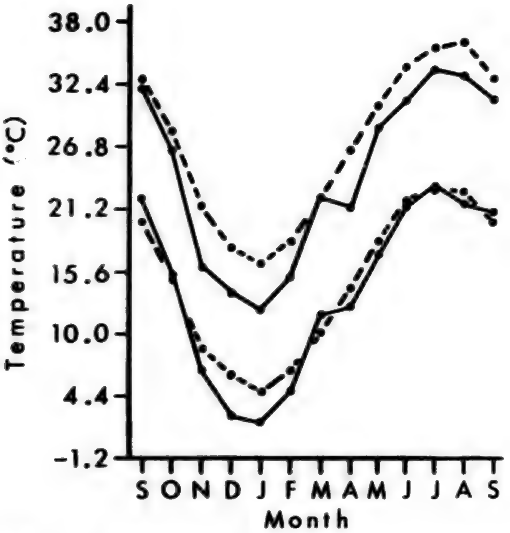

Fig. 2. Comparison of mean monthly temperatures of 1933–62 (dashed lines) to study period, September 1972–September 1973 (continuous lines). Two top lines indicate daily maximum means and two bottom lines indicate daily minimum means.

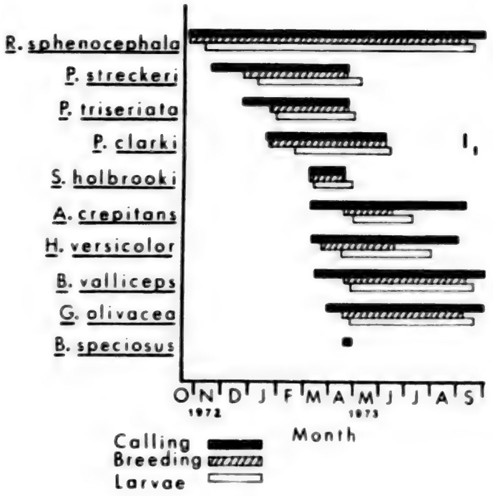

Fig. 3. Calling, breeding, and larval periods for each species during the 1972–73 study period.

Data for Texas monthly summaries, and from Climatological Summary for 1933 to 1962, both prepared by the U.S. Department of Commerce). Mean monthly temperatures were below normal during most of the study (Fig. 2). The study took place during a year which was unique in two ways to Brazos County. Two snowfalls (9 January and 8 February) occurred with appreciable accumulation, the first record of snow accumulation twice in one winter. More importantly, rainfall during the study was far above normal compared with previous years (Fig. 1). Total precipitation for Brazos County in the calendar year 1973 was 1,510 mm, which was only slightly less than the greatest recorded annual rainfall (1,577 mm).

Rainfall amounts during the study period were recorded as follows: 1,417 mm at Easterwood Airport Weather Station, 1,308 mm at Texas A&M University Weather Station, and 1,469 mm at the home of Dr. Dixon. Abundant precipitation during most of the study provided those anurans using temporary ponds with an excellent opportunity to achieve their breeding potential.

Results

A detailed account for each species' calling, breeding, and larval periods, including the relation of air temperatures and rainfall to reproductive activities throughout the year, was given by Wiest (1974). The data clearly indicated that the calling and breeding peaks of each species were closely associated with periods of rainfall. Tables 1 and 2 summarize the environmental correlates of calling and breeding periods.

The anuran vocalization sequence, based on the first evening when calling was heard, was as follows: *Pseudacris streckeri* vocalized first, followed by *P. triseriata*, *Scaphiopus holbrooki*, *Acris crepitans*, *Hyla versicolor*, *Bufo valliceps*, and *Gastrophryne olivacea* (Fig. 3). Exceptions to this pattern were *R. sphenocephala*, which called in practically every month of the year, and *P. clarki*, which had a primary calling period in the winter-spring months and a short opportunistic calling period in late summer. *Bufo speciosus* and *B. woodhousei* are uncommon in the study area and were observed only a few times. The reproductive patterns of each species as related to air temperatures (Fig. 4) suggest the same successional pattern as presented in Fig. 3.

Larval samples collected in three of the ponds were sufficient to summarize the larval succession pattern for all ponds. The biweekly summaries of larvae collected at these three ponds is given in Figs. 5, 6, and 7.

Table 1. *Calling statistics for each anuran species (air temperature and humidity at 2100 h; air temperature at 2.5 cm above ground).*

Species	No. of calling nights	Calling period	Temperature (°C)	Humidity (%)
Rana sphenocephala	87	21 Oct 72–27 Sep 73	3.0–26.1 $\bar{x}$ = 17.3	39 – 100 $\bar{x}$ = 79
Pseudacris streckeri	89	15 Nov 72–18 Apr 73	1.8–21.8 $\bar{x}$ = 12.1	39–100 $\bar{x}$ = 76
P. triseriata	84	20 Dec 72–19 Apr 73	-2.5–22.0 $\bar{x}$ = 12.8	39 -100 $\bar{x}$ = 76
P. clarki	60	16 Jan 73–5 Jun 73; 5–6 Sep 73	3.0–23.2 $\bar{x}$ = 14.5	39–100 $\bar{x}$ = 78
Scaphiopus holbrooki	5	6 Mar 73–15 Apr 73	13.0–18.0 $\bar{x}$ = 16.1	63–100 $\bar{x}$ = 75
Acris crepitans	85	6 Mar 73–6 Sep 73	8.7 – 28.3 $\bar{x}$ = 20.1	49–100 $\bar{x}$ = 77
Hyla versicolor	51	7 Mar 73–27 Aug 73	13.0–28.1 $\bar{x}$ = 21.8	51–100 $\bar{x}$ = 81
Bufo valliceps	44	12 Mar 73–27 Sep 73	18.5–28.3 $\bar{x}$ = 23.0	62–100 $\bar{x}$ = 81
Gastrophryne olivacea	34	26 Mar 73–27 Sep 73	11.3–27.2 $\bar{x}$ = 21.7	65–100 $\bar{x}$ = 85
Bufo speciosus	6	7–22 Apr 73	18.5–23.1 $\bar{x}$ = 20.8	88–100 $\bar{x}$ = 93

Table 2. *Breeding statistics for each anuran species (air temperature and humidity taken at 2100 h; air temperature at 2.5 cm above ground).*

Species	No. of breeding nights	Breeding period	Temperature (°C)	Humidity (%)	Larval period
Rana sphenocephala	17	22 Oct 72–5 Sep 73	11.8–25.7 $\bar{x}$ = 17.8	68–100 $\bar{x}$ = 84	8 Nov 72–16 Sep 73
Pseudacris streckeri	25	20 Dec 72–17 Apr 73	4.2–19.8 $\bar{x}$ = 13.5	63–100 $\bar{x}$ = 83	31 Dec 72–12 May 73
P. triseriata	21	19 Jan 73–17 Apr 73	6.7–19.9 $\bar{x}$ = 14.8	62–100 $\bar{x}$ = 79	27 Jan 73–28 Apr 73
P. clarki	11	20 Jan 73–5 Sep 73	11.8–21.3 $\bar{x}$ = 17.8	68–100 $\bar{x}$ = 84	17 Feb 73–9 May 73; 16 Sep 73
Scaphiopus holbrooki	5	6 Mar 73–15 Apr 73	13.0–18.0 $\bar{x}$ = 16.1	63–100 $\bar{x}$ = 75	10 Mar 73–24 Apr 73
Acris crepitans	5	17 Apr 73–12 Jun 73	18.5–23.2 $\bar{x}$ = 21.1	65–100 $\bar{x}$ = 88	28 Apr 73–14 Jul 73
Hyla versicolor	6	18 Mar 73–14 Jun 73	18.5–25.4 $\bar{x}$ = 21.6	75–100 $\bar{x}$ = 86	14 Apr 73–28 Jul 73
Bufo valliceps	16	17 Apr 73–6 Sep 73	18.5–27.2 $\bar{x}$ = 22.1	70–100 $\bar{x}$ = 84	24 Apr 73–16 Sep 73
Gastrophryne olivacea	10	15 Apr 73–5 Sep 73	18.0–26.7 $\bar{x}$ = 22.0	70–100 $\bar{x}$ = 87	24 Apr 73–16 Sep 73

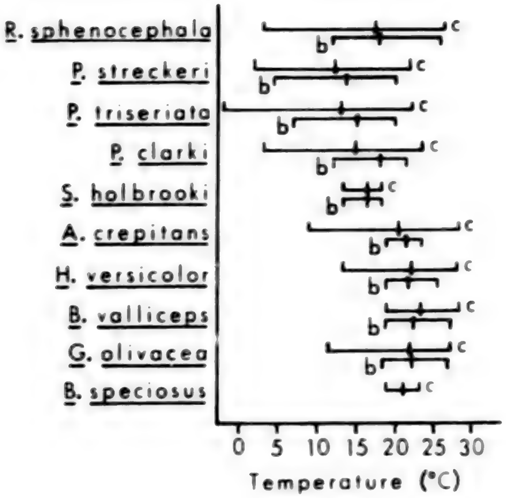

Fig. 4. Ranges and means of air temperatures (2100 h) on nights of calling (= c) and breeding (= b) for each species.

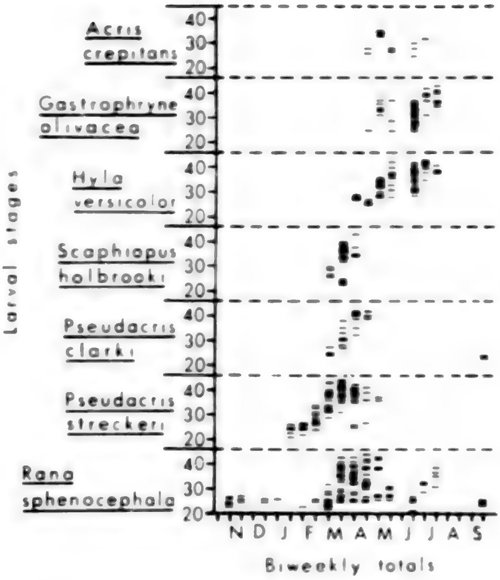

Fig. 5. Biweekly summaries of larval developmental stages from all larvae collected in pond D. Individual dashes represent larval stages (Gosner 1960), and the dashed horizontal lines indicate metamorphosis (stage 46).

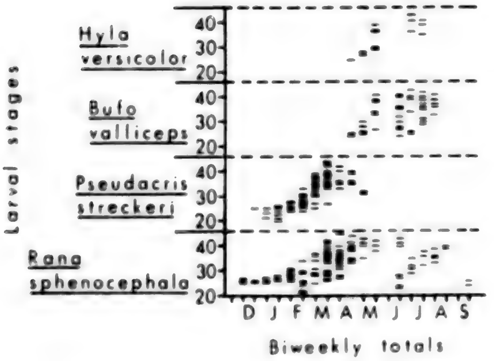

Fig. 6. Biweekly summaries of larval developmental stages from all larvae collected in pond G. Individual dashes represent larval stages (Gosner 1960), and the dashed horizontal lines indicate metamorphosis (stage 46).

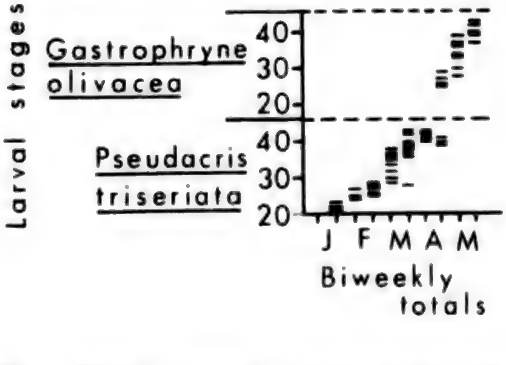

Fig. 7. Biweekly summaries of larval developmental stages from all larvae collected in pond J. Individual dashes represent larval stages (Gosner 1960), and the dashed horizontal lines indicate metamorphosis (stage 46).

Species Excluded from Study

Not all anuran species occurring in Brazos County were incorporated into this study because some used only permanent bodies of water for breeding, and a few were too rare to study in detail. *Hyla cinerea* was observed calling only at permanent ponds between 23 April and 1 August 1973. *Rana areolata*, *R. catesbeiana*, *R. clamitans*, and *R. palustris* use permanent bodies of water. Of these four species, only *R. catesbeiana* was heard calling (23 April to 10 August 1973). *Gastrophryne carolinensis* breeds in temporary ponds, but was not observed in the study area. However, during summer observations this species was common along the bottomlands of the Navasota River, Brazos County. Since *G. carolinensis* exhibits a mesic-adapted breeding pattern (Blair 1955), it possibly remains in moist forested regions which would explain its absence from the less forested upland study areas.

Post-Study Observations of Ponds

Following the wet study period, a post-study inspection of each pond was made on 2 March 1974 during an especially dry period. At this time one of the ponds had been filled in by construction work and four others were completely dry. Of the seven ponds that had water, only three approximated the dimensions and depths seen during the study period. These observations emphasize the instability characteristic of temporary ponds.

Discussion

Calling in *Rana sphenocephala* was generally initiated by rainfall when maximum daily temperatures were above 15.0°C. This species has a winter–spring breeding season (8 February to 13 May) and a fall breeding season (22 July to 14 October) in the Austin, Texas, area (Blair 1961). The same winter–spring and fall seasons apply to the observed breeding dates in the present study (winter–spring from 17 January to 12 June; fall from 5 September to 27 November). Data from these two studies suggest that breeding can occur in any month of the year. Blair (1961) also stated that the winter–spring and fall breeding periods appeared to be of about equal importance in terms of maintenance and replacement of the population. My study suggests that the winter–spring period is more significant, since many more amplectic pairs and egg masses were seen during this period; this species is more of an opportunistic and sporadic breeder in the fall.

Although all three species of *Pseudacris* are winter breeders and overlap in their reproductive seasons, they initially appeared at slightly different times of the year. *Pseudacris clarki* was clearly less tolerant of low temperatures than either *P. streckeri* or *P. triseriata*. Substantial rainfall and a drop in air temperature, followed by a sudden rise in temperatures, generally led to calling peaks and egg deposition in *Pseudacris* during the temperature rise. *Pseudacris clarki* showed more of a preference for shallow grassy pools than either *P. streckeri* or *P. triseriata*. *Pseudacris streckeri* was observed calling with *P. clarki* and *P. triseriata*, but *clarki* and *triseriata* were never heard calling from the same breeding ponds. *Pseudacris clarki* had a delayed breeding period in September which could be a population response to the possibility of spring drought as suggested by Kennedy (1958), or it could simply represent a response to weather conditions similar to those during the late stages of the normal spring breeding period. Egg masses of *Pseudacris* were attached to vegetation well below the water's surface which was a definite advantage when ice covered the ponds on several occasions.

Calling and breeding in *Scaphiopus holbrooki* coincided on five nights in March and April. My data suggest that low temperatures, possibly maximum daily temperatures below 18.9°C, inhibited breeding even when there had been sufficient rainfall. The largest choruses and most extensive breeding occurred on the evening of 15 April (maximum daily temperature = 20.6°C) following a steady rain of 52 mm. Rainfall of 40 mm and a maximum daily temperature of 17.2°C on 17 April failed to initiate calling. My data also agree with those of Wasserman (1957) who found no *S. holbrooki* breeding after May during 4 years of study in Texas. Bragg (1967) suggested that not all adult females in an area produce eggs each time breeding conditions are favorable. A staggering of egg production over several months takes advantage of all favorable situations. Possibly a related phenomenon in my study was the fact that on five occasions following breeding periods, gravid females were found near breeding ponds on evenings when calling did not occur.

Acris crepitans was active over a wide range of temperatures and was seen in every month of the study, but this species only called in the spring and summer. This anuran usually inhabits permanent bodies of water, but also frequents temporary ponds when sufficient water is available. Calling peaks extended through three periods: 12-19 March, 12 April-14 May, and 4-18 June. Contrary to Blair (1961), my study indicates that calling peaks were generally associated with periods of heavy rainfall. Five nights of breeding between 17 April and 12 June in my study paralleled the breeding season noted by Pyburn (1958) and Blair (1961) at other Texas localities.

Hyla versicolor was not particularly common, probably because of the lack of trees in most of the study area. Trees are generally used as calling stations and play a major role in the breeding behavior of this species. Maximum daily temperatures below 20°C and evening temperatures below 16 – 18°C generally inhibited calling. Most calling and breeding were observed during periods of rainfall or high humidity (above 80%).

Bufo valliceps is one of the most common anurans in the study area. Blair (1960) placed emphasis on rainfall as the main initiating factor for calling in this species. My data clearly indicate that evening air temperatures below 18.5°C inhibited calling, particularly at the start of the calling season. Rainfall only became important for calling and breeding when evening temperatures were consistently above 20.0°C after mid-May. Similarly, Thornton (1960) found that sufficient rains during the breeding season did not bring out choruses of *B. valliceps* if temperatures were below 16.1°C.

Although *Bufo woodhousei* is supposedly distributed in all of east-central Texas (Stebbins 1954; Raun and Gehlbach 1972; Conant 1975), I observed this species on only a few occasions and I never heard it calling. However, during the summer of 1973, large numbers of *B. woodhousei* were encountered along the Navasota River bottom. The floodplains and lowlands along the river had sandy soils and in general were unaltered by man. This observation agrees with that of Axtell (1963), who proposed that *B. woodhousei* was not widely distributed throughout the arid Southwest, but was highly restricted to localized, stream edge habitat.

Gastrophryne olivacea was probably one of the most opportunistic breeders associated with periods of rainfall. My data indicate that air and water temperatures below 18.0°C were important factors inhibiting calling. Warm rains were necessary for initiating reproductive activities in this species.

Bufo speciosus was only observed calling on six consecutive evenings from shallow temporary pools that were formed from the overflow of an old cattle tank. Blair (1964) suggested that *B. speciosus* requires extensive (flooding) rainfall which is an adaptation for existence in the xeric Southwest. This requirement for flooding was fulfilled on numerous occasions during the study and does not afford an explanation for the limited emergence of this species. Perhaps the population numbers are so low in this marginal habitat that extensive calling and breeding are not possible.

Data collected on reproductive activities clearly indicate a successional occurrence for anurans using temporary ponds in Texas (Fig. 3). There are four basic groups of anurans that make up this sequential pattern. The first is *Rana sphenocephala*, which is active throughout the year. The second component consists of winter–spring breeders, *Pseudacris streckeri*, *P. triseriata*, and *P. clarki*. The third component is *Scaphiopus holbrooki*, with distinctively short calling, breeding, and larval periods in the spring only. The last group consists of *Acris crepitans*, *Hyla versicolor*, *Bufo valliceps*, and *Gastrophryne olivacea*, which are most active during spring–summer months. Although there was overlap of the reproductive seasons of these species, there was an obvious temporal partitioning of the ponds. Different combinations of species occurred in each pond, and spatial separations existed between those species that were active at the same time of the year.

Males of each species initiate the calling period, and the presence of adult females determines the breeding period. Breeding periods of all species were within the broader calling periods, except in *S. holbrooki*, whose calling and breeding periods coincided. Since much more calling than breeding occurred, these data suggest that some energy is wasted on the part of males of some species. It is generally accepted, however, that calling attracts conspecific females to breeding ponds. Males of some species have been observed calling long before females arrived to breed, and this calling may have been important in attracting other males to the pond, thus increasing the number of males at a given breeding locality. If a certain "calling volume" is necessary to attract females to the breeding pond, this increased population of calling males would be advantageous. Although this is only conjecture, the importance of calling is an unsettled question and needs to be further explored.

The range of air temperatures on nights of calling and on nights of breeding coincide in *S. holbrooki*. For all other anurans the air temperature range on calling nights is greater than on breeding nights. This suggests that females wait for certain optimal breeding conditions, in this example a narrower range of air temperatures within the range of calling males. Although not significantly different in some species, the mean humidity is higher on breeding nights than on calling nights, suggesting that females require slightly higher humidities for breeding than males need for calling.

Larvae of each species were present over a slightly different time span and various combinations of larvae occurred in the ponds (Figs. 5, 6, 7). *Rana sphenocephala* larvae probably occur in temporary ponds throughout the year when water is available. Late April was a transitional period between the end of the winter–spring larvae (*P. streckeri*, *P. triseriata*, *P. clarki*, *S. holbrooki*) and the beginning of the spring–summer larvae (*A. crepitans*, *H. versicolor*, *B. valliceps*, *G. olivacea*). At this time there were two classes of larvae, generally larger larvae of the winter-spring species and smaller larvae of the spring-summer species. *Pseudacris clarki* broke this pattern slightly by a short larval period in late summer. In terms of both individuals and species, the greatest number of larvae were present in April and May, and this larval bloom corresponds to the time of greatest rainfall. Because temporary ponds are generally susceptible to drying, there is a definite adaptive advantage for most larvae to be in the ponds during spring months.

Certainly year-to-year fluctuations in seasonal weather conditions will alter the pattern of anuran succession as discussed herein. Numerous climatic factors are contributing to the variation in each anuran's reproductive season, but data must be accumulated for many years before appropriate analyses can determine the influence of many of these factors. My interpretation of the environmental effects on each species' reproductive season was based on data from 1 year. This study indicates the importance of fluctuations in air and water temperatures, rainfall, and possibly humidity, as the overriding causes of variation in anuran reproductive patterns in Brazos County, Texas.

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Prey Patterns and Trophic Niche Overlap in Four Species of Caribbean Frogs

by

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Abstract

Frogs in the genus *Eleutherodactylus* make up the majority of species of anurans and a high percentage of all terrestrial vertebrates in the Caribbean Islands. To examine the factors regulating the species diversity of this group on various islands, I made observations on the diet, rates of feeding, and movement for four species from the Virgin Islands and Puerto Rico. Patterns in the diet generally agree with published accounts for communities of insects from the same area, suggesting that this assemblage of species consumes prey species in the proportion in which they occur. Estimates of the competitive coefficient show trophic niche separation for most species pairs by length or prey type, suggesting trophic niche partitioning.

Since frogs in the genus *Eleutherodactylus* make up a majority of Caribbean amphibians and a high proportion of all terrestrial insectivores, it is of interest to examine their patterns of use of the insect prey base.

Schoener and Janzen (1968) reported patterns in tropical foliage insect communities in several tropical areas of Costa Rica. The present study examines prey use of four species of frogs in the genus *Eleutherodactylus* and compares patterns from stomach analyses with the sweep net studies of Schoener and Janzen. Four species of *Eleutherodactylus* occur on the Virgin Islands, and two of these species also occur on Puerto Rico. Four of the major Virgin Islands and Puerto Rico were selected for this study. These five islands provide various combinations of the four species and provide a natural experiment in resource partitioning.

Methods

From September 1973 to June 1974 four species of frogs in the genus *Eleutherodactylus* were observed and collected on the Virgin Islands of St. Thomas, St. John, St. Croix, Tortola, and on Puerto Rico. Two of the species, *E. lentus* and *E. schwartzi* occur only on the Virgin Islands. The remaining two species, *E. cochranae* and *E. antillensis*, also occur on Puerto Rico. A collection of about 100 specimens was made for each species on each island. All specimens were preserved in the field within 2 h of capture.

Adults of each of the four species were observed while feeding and moving by means of a GTE Sylvania night-viewing device. This device allows observation under natural light conditions at night. Subjects were observed for periods of 15 min each. All feeding attacks and movements not associated with a feeding attack were tabulated. Each species was observed for 20 observational periods. The observations were made throughout the study at different times of the night and on various islands.

A small collection of insects which seemed likely to be included in the diet of *Eleutherodactylus* was made. Prey items removed from the frogs' stomachs were measured with an ocular micrometer disk inserted into a dissection microscope, compared with the initial insect col-

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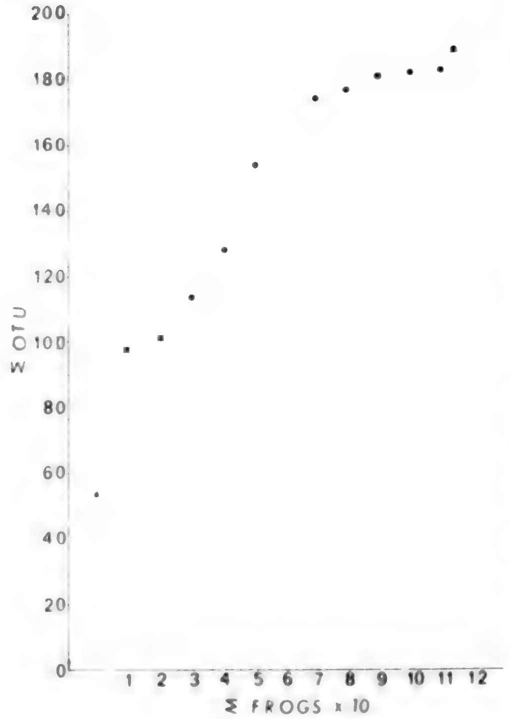

Fig. 1. Cumulative number of OTU's vs. number of frogs examined. The triangle indicates an initial reference collection. Curve was fitted by eye

lection, and identified by the collection number. Any prey item not represented in the reference collection was assigned a number and added to the collection. No attempt was made to associate larval stages with the corresponding adult stage. All prey items assigned the same reference collection number will be referred to as belonging to the same Operational Taxonomic Unit (OTU). Any OTU may contain several morphologically similar species, and different developmental stages of the same species may have been assigned to different OTU's. A total of 190 OTU's were assigned during the study. The number of prey species represented by the 190 OTU's is unknown, but the number of OTU's in any sample is probably directly proportional to the number of prey species.

Figure 1 is a line plot of the cumulative number of OTU's against the number of frogs examined. The figure suggests that additional collecting would have added few new categories. For each OTU from each frog's stomach, the total number, average length, and width were recorded. I calculated volume using the formula for a cylinder.

Results and Discussion

Natural History

Eleutherodactylus antillensis (mean snout-vent lengths in mm: males 23, females 27), *E. cochranae* (males 18, females 19), and *E. schwartzi* (males 24, females 29) are very similar in appearance and in general behavior. All three species call and forage mostly on foliage. Individuals use the same foraging and resting sites over long periods of time. *Eleutherodactylus lentus* (males 22, females 30) is similar to the other three species, except that the toe disks are reduced and the males are mute. This species was found exclusively on the ground. Individuals move frequently and are apparently not faithful to any given locality. The basic foraging strategy of *E. lentus* differs from that of the other three species. For convenience, *E. lentus* will be termed a searcher and the other species as sit-and-wait predators.

General Prey Patterns

Schoener and Janzen (1968) found that, in general, sizes of insects from sweep samples fit a lognormal distribution. If the four *Eleutherodactylus* species used in the present study consume prey items in the proportion in which those items occur, one would expect that the prey items removed from all of the specimens would also approximate a lognormal distribution. A histogram of all of the prey items appears to fit a lognormal distribution (Fig. 2).

Schoener and Janzen (1968) demonstrated that logarithmic transformation produced a distribution closer to normality than did the original measurements. They showed that the g_1, g_2, and a χ^2 statistic measuring the departure from normality are smaller in the transformed data. In the present study (Table 1) the logarithmic transformation produced g_1 and g_2 values which are closer to zero, but the curve remains leptokurtic and skewed to the right. The χ^2 statistic is smaller than in the nontransformed data indicating less departure from normality.

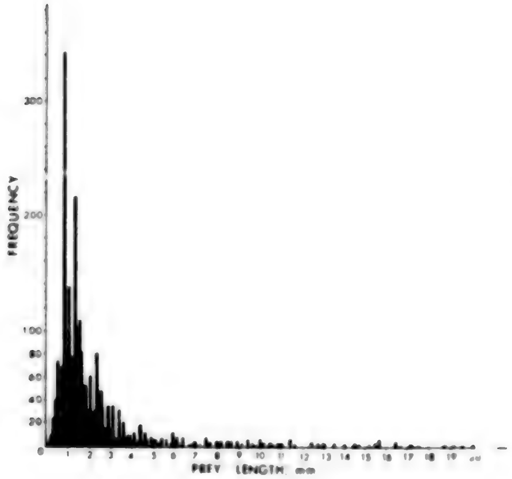

Fig. 2. Histogram of all prey items removed from stomach contents.

Table 1. *Statistical features of prey items removed from stomach contents of* Eleutherodactylus *from Puerto Rico and the Virgin Islands.*

Data	Mean	SD	g_1	g_2	χ^2
Length					
Raw (mm)	2.7	2.6	5.0	50.5	14.511.3
Transformed	0.80	0.48	0.87	1.71	1.077.8
Volume					
Raw (mm^3)	10.8	7.5	1.9	4.5	136.8
Transformed	2.19	0.58	-0.27	2.63	19.7

These results indicate that the length and volume of prey species fit a lognormal distribution better than a simple normal distribution. The g_1 and g_2 values indicate that there are more large prey items than expected. These results are in agreement with the results of the sweep sample study of Schoener and Janzen (1968).

Prey Taxa

The four species of *Eleutherodactylus* studied are general arthropod predators, but they occasionally take other animals. From site to site species vary in the proportions of their diets drawn from different taxa (Table 2). On St. John, 70.1% of the prey items of *E. antillensis* are ants, but on Puerto Rico only 11.7% of the items are ants. On St. John, 44.1% of the prey items of *E. cochranae* are spiders, but on Puerto Rico only 3.5% are spiders.

Diet Overlap

Mutual use of food resources implies the potential for competition. It is not, of course, evidence for competition at any specific time. The data for mutual use of food items by OTU (Table 3) show

Table 2. *Percentage of total individuals (I) and total volume (V) of various prey taxa.*

	Puerto Rico				St. John			
	E. antillensis		*E. cochranae*		*E. antillensis*		*E. cochranae*	
Order	I	V	I	V	I	V	I	V
Hymenoptera								
Formicidae	11.7	14.3	13.4	11.5	70.1	22.1	12.0	5.4
Other	0.0	0.0	0.4	0.1	2.6	0.2	0.0	0.0
Diptera	15.8	3.5	13.0	23.0	3.9	3.4	0.4	2.2
Coleoptera	14.8	23.8	1.0	0.3	6.0	3.5	5.7	6.3
Isoptera	0.0	0.0	0.0	0.0	0.0	0.0	2.1	0.2
Homoptera	32.8	3.4	62.7	43.4	3.9	1.2	3.9	2.4
Hemiptera	4.6	4.0	1.4	12.0	0.9	8.2	2.7	7.8
Lepidoptera	3.3	13.6	0.0	0.0	2.1	23.5	3.0	2.5
Orthoptera	1.0	22.8	0.0	0.0	3.0	12.6	11.1	52.4
Acarina	0.0	0.0	3.5	0.4	0.0	0.0	0.0	0.0
Isopoda	0.5	0.2	1.1	0.9	0.9	0.1	10.2	17.1
Mollusca	0.3	7.5	0.0	0.0	0.8	0.0	0.0	0.0
Araneae	4.3	6.0	3.5	5.2	5.6	0.3	44.1	1.3
Unidentified	10.9	0.9	0.4	3.4	1.3	22.2	0.1	0.2

Table 3. *Diet by OTU of* Eleutherodactylus *from Puerto Rico and the Virgin Islands.*

Island, and species of *Eleutherodactylus*	Number of OTU's		Number of prey items	
	Total	Shared	Total	In shared OTU's
Puerto Rico				
antillensis	56	21	387	300
cochranae	31	21	284	263
St. Thomas				
antillensis	54	42	221	206
cochranae	53	41	952	921
lentus	81	51	1,627	1,506
St. John				
antillensis	43	19	333	209
cochranae	37	19	234	194
St. Croix				
antillensis	43	22	136	59
lentus	62	22	918	202
Tortola				
antillensis	44	26	220	184
schwartzi	51	31	415	344
*cochranae**	15	14	39	38

*Sample based on 30 individuals only

that all four species share some of the same OTU's with one or both cogeners, and the shared categories clearly contain the majority of individual prey items for all of the species.

On Puerto Rico the diet of *E. antillensis* consisted of 56 OTU's. Thirty-five of these were not found in the diet of *E. cochranae*. The diet of *E. cochranae* consisted of 31 OTU's, only 10 of which were not found in the diet of *E. antillensis*. In the Virgin Islands, the diet of each of the two species included 50% of the OTU's that were being used solely by the other species on Puerto Rico. Only two of the 21 OTU's that were shared on Puerto Rico occurred uniquely in the diet of one of the species on the Virgin Islands. Both instances involve a small number of individuals, and this could be the result of chance. The most significant aspect of these results is the increase in the number of OTU's shared on the Virgin Islands.

An overlap in the diet of two species may be of little importance if the prey involved constitute a minor fraction of the energy budget of one or both of the species. Assuming that the energetic return is directly proportional to the prey volume, the most common items contain little volume, and presumably little caloric value. In general for the sit-and-wait frogs a few large items contain the major portion of the volume. Based on this, one might expect that some aspect of the morphology of these frogs, such as head width, would be related to these few large categories.

Figure 3 shows a regression line, fitted by Bartlett's three-group method, for head width and modal prey volume. Each sex of each species from each island is plotted separately. The correlation for these two variables is 0.623 ($P < 0.01$).

Figure 4 is a modified copy of Fig. 3, omitting *E. lentus* and with the sit-and-wait species on each island joined by a line. The shape of the lines suggests that the relation between mean head width and modal prey volume is not rectilinear. The distance between lines suggests that there is some amount of inter-island variation in the availability of prey sizes.

Assuming that the prey base for *E. lentus* and the sit-and-wait frogs is the same, as suggested by overlap of OTU's, the differences seen in Fig. 3 could be attributed to a difference in foraging strategy.

Feeding Rates

Feeding rates were obtained in two different

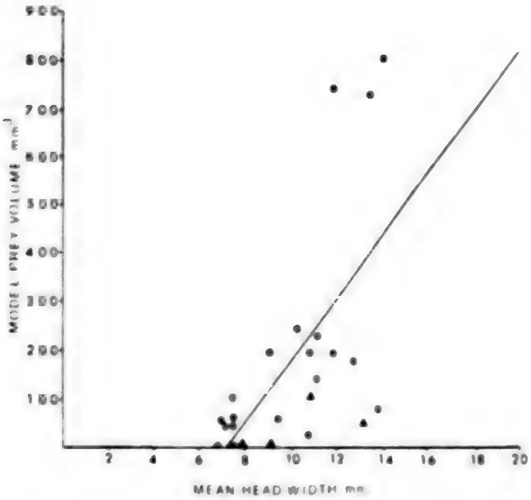

Fig. 3. Regression line for mean head width of both sexes of each species to modal prey volume in the diet. Triangles indicate *E. lentus*, circles indicate remaining three species.

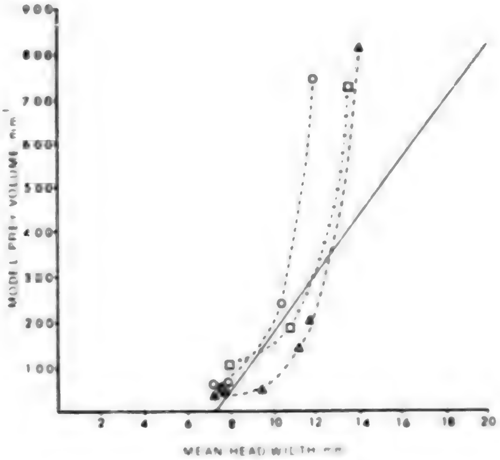

Fig. 4. Head width vs. modal prey volume for sit-and-wait frogs on three islands. Tortola (triangles), St. Thomas (circles), and St. John (squares).

ways: (1) feeding was observed directly by means of the night-viewing device, or (2) the number of prey items recovered from each collected specimen was divided by the elapsed time from dusk to capture. The second method is likely to be an underestimate of the total feeding rate, especially for specimens captured shortly before dawn. The rate at which items are transported out of the stomach is unknown, but frogs captured during the first few minutes after dark and those captured a few hours after dawn uniformly lack prey in the stomach. This suggests that feeding does not occur before dark, and that all items were moved from the stomach within a few hours after dawn.

The average feeding rate obtained by stomach analysis for *E. antillensis* was 0.8 prey/h, for *E. schwartzi*, 1.2 prey/h, and for *E. cochranae*, 1.5/h. This suggests an inverse relation between feeding rate and size within the sit-and-wait frogs. The average feeding rate for *E. lentus* was 2.8 prey/h, which is two to three times the rate of a sit-and-wait frog of the same size.

The average observed feeding rate for *E. antillensis* was 1.0 prey/h and the average nonfeeding movement rate was 1.0 move/h. The average observed feeding rate for *E. schwartzi* was 0.95 prey/h and the average movement rate was 1.2 move/h. The average observed feeding rate for *E. cochranae* was 2.2 prey/h and the average observed movement rate was 1.4 move/h. The average observed feeding rate for *E. lentus* was 2.6 prey/h and the average movement rate was 2.4 move/h.

The two methods of estimating feeding rates yield similar results for all four species, suggesting that neither method is strongly biased. The movement rates are also inversely related to size of animal within the sit-and-wait frogs. The *E. lentus* average movement rate is two to three times the rate of a sit-and-wait frog of the same size.

Niche Overlap

The extent to which resource use of one species overlaps that of another is a measure of possible competition between the species. Although several measures of overlap are available, it is perhaps most meaningful to measure niche overlap in terms of estimates of the competitive coefficient alpha (α).

Levins (1968) and MacArthur (1972) provided formulae for estimation of alpha based on a single resource (see Estimates of Alpha, the Competition Coefficient). Levins' formula lends itself to discrete data, whereas MacArthur's formula is more appropriate for continuous data. MacArthur's formula has the disadvantage of assuming that each species would exert the same degree of effect on the other ($\alpha_{12} = \alpha_{21}$). This is true only if the variance of resource utilization is equal.

Table 4. *Alpha estimates for prey use by Antillean* Eleutherodactylus. *Resource axes are prey length and prey OTU.*[a] *Alpha is read as the effect of the horizontal species on the vertical species. Intraspecific alpha is the effect of female on male.*

Locality, and species of *Eleutherodactylus*	Species of *Eleutherodactylus*							
	antillensis		*cochranae*		*lentus*		*schwartzi*	
	Length	OTU	Length	OTU	Length	OTU	Length	OTU
St. Thomas								
antillensis	0.95		0.87	0.35	0.97	0.26		
cochranae	0.87	0.30	0.95		0.90	0.77		
lentus	0.97	0.42	0.90	1.29	0.84			
Tortola								
antillensis	0.95		0.76	0.32			0.95	0.15
cochranae	0.76	0.15	0.89				0.91	0.19
schwartzi	0.95	0.20	0.91	0.57			0.88	
St. John								
antillensis	0.90		0.85	0.90				
cochranae	0.85	0.62	1.00					
Puerto Rico								
antillensis	0.97		0.97	0.07				
cochranae	0.97	0.07	0.98					
St. Croix								
antillensis	1.00				0.96	0.44		
lentus	0.96	0.83			0.62			

[a] OTU = operational taxonomic unit.

The two most likely dietary variables are length of prey and prey OTU's. Length is a continuous variable, whereas prey OTU's are discrete. The alpha estimate was computed by MacArthur's and Levins' formulae, respectively, but there are some problems in computation and interpretation of each estimate. The prey length alpha is based on frequency, whereas the prey OTU alpha is based on volume. The prey length alpha ignores the potential separation by specific type prey, and the prey OTU alpha may be underestimated because of the small sample size of the larger prey items. Finally, each frog species is treated as a homogeneous group, when in fact each sex might be acting to some unknown degree as an "ecospecies." As an indication of this effect, an intraspecific alpha estimate was computed for each dietary variable, treating the sexes as separate groups (Table 4). The prey OTU alpha estimate is omitted from the intraspecific comparisons because of small sample sizes. Within each set of interspecific alpha estimates, there are often one or more low values which indicate niche separation.

Estimates of Alpha, the Competition Coefficient

1. From Levins (1968):

   $\alpha_{ij} = \sum_h P_{ih} P_{jh} / \sum_h P_{ih}^2$, where P_{ih} is probability of species i occurring in resource cell h and P_{jh} is the probability of species j occuring in cell h. In this paper, the resource cells, h, are the prey OTU's. Levins' α can be as low as 0 (no overlap) and ordinarily does not exceed 1.5.

2. From MacArthur (1972):

   $\alpha = e \exp [-d^2/2(\sigma_1^2 + \sigma_2^2)]$, where σ_1 and σ_2 are the standard deviations of the resource distributions for species 1 and 2, and d is the distance between the means of these distributions. In this estimate, it is assumed that α_{12} (the effect of species 2 on species 1) equals α_{21} (the effect of species 1 on species 2). In this paper, the resource distributions are the frequency distributions of the prey lengths. MacArthur's α varies between 0 (no overlap) and 1 (complete overlap).

Conclusions

The general agreement between the sweep net sample data of Schoener and Janzen (1968) and the stomach content data in the present study indicates that all four species of *Eleutherodactylus* consume foliage insects in the proportion in which the insects occur. The lengths of insects tend to fit a lognormal distribution which is leptokurtic and skewed to the right. This indicates that a larger number of large insects exists in the combined diets than would be predicted by a lognormal distribution.

Within the four species of frogs, *E. lentus* uses a basically different foraging strategy. *E. lentus* is an active ground-dwelling species which moves and feeds two to three times faster than the other three species. The remaining three species are mostly foliage dwellers. Within this group there is an inverse relationship between size and the rates of feeding and movement.

In the comparison of intraspecific sets, one or more low values indicate trophic niche separation.

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SNAKE COMMUNITIES

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Niche Dimensions and Resource Partitioning in a Great Basin Desert Snake Community

by

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Abstract

Aspects of the population biology and community ecology of three sympatric species of snakes (*Coluber constrictor*, *Masticophis taeniatus*, and *Pituophis melanoleucus*) using communal dens in a Great Basin cold desert shrub habitat were studied in northern Utah between 1969 and 1973. Food habits analysis and telemetric tracking of snakes in the field allowed quantification of the food and place dimensions of the ecological niche of each species. We also report on thermal preferences, temporal overlap at hibernacula, annual body weight changes, and survivorship of these species. Species abundance distributions and species diversity in 10 North American snake communities are surveyed.

The species were separated strongly by food habits. Major prey taken were insects (*Coluber*), lizards (*Masticophis*), and mammals (*Pituophis*). *Coluber* had the narrowest food niche, *Pituophis* was intermediate, and *Masticophis* had the broadest niche. In summer, *Masticophis* had the broadest place niche and differed from *Coluber* and *Pituophis*, which were underground most often. All three paired species comparisons showed the average overall niche overlap values were 0.79 (place) and 0.19 (food). The trophic dimension is more important in resource partitioning than is the spatial dimension for snakes in this community. Complementarity between these two niche dimensions exists.

Snakes, as a group, had lower mean activity temperatures than lizards at our study locality. Thermal preferences underground (26-27°C) were very similar among the snakes. *Pituophis* had a lower mean activity temperature (28°C) than *Coluber* and *Masticophis* (31-32°C) on the surface. At dens during spring emergence and autumn ingress, when competitive interactions may have been possible, most *Masticophis* and *Pituophis* arrived at and emerged from dens 2-3 weeks earlier than *Coluber*, but this "separation" may be more closely associated with species differences in reproductive behavior and dispersal than with competition.

Annual survival rates were similar in the three species: first-year survivorship ranged from 15 to 20% and adult survivorship ranged from 63% (*Pituophis*) to 78% (*Coluber*) and 80% (*Masticophis*). Maximum life expectancies are 16 years for *Pituophis* and 20 years for *Coluber* and *Masticophis*, according to these schedules.

Proportions of snakes that increased in body weight during 3 years varied between species. About 90% of *Masticophis* increased each year. In the other two species, 1 year each was unfavorable for *Pituophis* (1971, a wet year) and *Coluber* (1972, a dry year) when only 64-68% gained weight compared with favorable years when 83-98% of these snakes gained weight. Causal factors responsible for these different environmental responses are probably related to the proportion of rain falling during the summer months

Rainfall may directly affect the snakes' water balance or the productivity of their prey populations. These effects probably act in different ways for each species and with different time lags through poorly understood and complex mechanisms.

Human predation has greatly altered the species composition at our desert study site over a 30-year time span, causing an almost complete shift in the dominant species (*Crotalus* and *Masticophis* in 1940, *Coluber* and *Pituophis* in 1970). At each time the diversity indices were similar (H = 0.99 in 1940's, H = 1.05 in 1970's) indicating that the replacements may be correlated with resource partitioning within the community.

In 1974 an extensive range fire destroyed the habitat around the communal dens. Subsequently, drifting sand buried the dens, completing an apparent extirpation of the snake community.

A number of studies have provided herpetological ecologists with sound biological data on single species of snakes, or have been autecological in focus (Fitch 1960, 1963, 1965, 1975; Hall 1969; Clark 1970, 1974; Brown 1973; Branson and Baker 1974; Clark and Fleet 1976) and several have dealt with two species (Platt 1969; Saint Girons 1975; Parker and Brown 1980). Only a few early studies attempted to compare three or more sympatric species (Fitch 1949; Carpenter 1952; Fouquette 1954; Fleharty 1967) and had a community outlook. Because they preceded the recent rapid growth of investigations into resource partitioning over the past 10 years or so (cf. Schoener 1974), none is couched in terms of a modern quantitative approach to community analysis, i.e., niche dimensionality and resource partitioning.

In addition to field studies cited above, some workers have explored broader patterns governing the structure of assemblages of snakes. Barbault (1970, 1971) examined population densities, biomass, and seasonal abundance of a snake fauna of a single geographic region and later analyzed these snake populations in a community context, particularly trophic relations (Barbault 1974). Other recent approaches to herpetological community studies of snakes largely have concerned food resources (Henderson 1974; Mushinsky and Hebrard 1977; Fitch, this volume) and at least three studies have treated both diet and habitat (Shine 1977; Hart 1979; Reynolds and Scott, this volume). Renewed interest in geographical patterns of species abundance and diversity was kindled largely by MacArthur (1965, 1972). Turner (1961) summarized data on relative abundance of snakes and Arnold (1972) analyzed snake community patterns to determine whether prey species density affects predator (snake) species density. Investigators seem now to be on the verge of considering the role of snakes in community structure as begun by Barbault (1974), Henderson (1974), Shine (1977), and Hart (1979). Although Schoener (1974) warned that merely documenting differences between species with respect to resource partitioning appeals only minimally to our scientific interests, perhaps we must settle for this level of description at present because our knowledge of snakes has lagged substantially behind that of other groups of vertebrates such as birds and lizards.

For 4 years (autumn 1969 through spring 1973) we studied the natural history and ecology of snakes using communal dens in a Great Basin cold desert shrub habitat in northern Utah. Results from these studies and a description of the study area are provided by Parker and Brown (1973) and Brown and Parker (1976*a*). We attempt to integrate some of our findings on racers, *Coluber constrictor* (Brown 1973; Brown and Parker 1982), whipsnakes, *Masticophis taeniatus*, and gopher snakes, *Pituophis melanoleucus* (Parker and Brown 1980) with emphasis on the ecological niche of these species. Although five additional less common species have been recorded at our snake dens, we gathered data primarily on these three most abundant species. Our studies provide a data base for treating these three species as a sympatric group making up the bulk (98% by numbers, 96% by biomass) of this snake community.

We examine aspects of the biology of the three species that bear on the following questions: (1) What dimensions of the ecological niche appear to be critical and how strongly are resources partitioned? (2) Do quantitative measures of overlap among paired species comparisons imply possible interspecific competiton? (3) In what ways do these snake species vary in their response to annually changing environmental conditions? (4)

How might any such differential response, along with the observed turnover in species composition and abundance in the community, reflect the ecological niche of each, and what might this tell us about community structure and population stability in snakes?

We definitely need empirical, quantitative field studies of snakes that might make this relatively specialized and morphologically homogeneous group more useful in broadening the theory of the ecological niche and of community structure in general. Whether this group of cryptic and difficult-to-study vertebrates can be used to accomplish this end remains to be seen. For many workers, snakes have proved to be attractive as research organisms. We hope to show here that they may also contribute substantially to a rapidly growing body of ecological knowledge at the community level.

Methods

Snakes were captured in spring and autumn by erecting screen wire fences around the snakes' hibernacula. Our general techniques, location of the study area, description of vegetation in the habitat (Great Basin cold desert shrub), and photographs of two of the dens and surrounding sagebrush flats, are provided by Brown and Parker (1976*a*). We recorded more than 1,400 individuals of seven species. Each snake was permanently marked at its first capture by clipping ventral scutes (Brown and Parker 1976*b*). Yearly individual body weight changes were based on successive spring or successive autumn captures that included one intervening period of winter dormancy. Inter-year variation in annual weight loss during hibernation was not significant in *Coluber* (Brown and Parker 1982) and *Pituophis* (Parker and Brown 1980) so both intervals used for determining body weight changes in these species (spring-to-spring or autumn-to-autumn) were equivalent. *Masticophis* weights were obtained at successive early spring captures, providing the most reliable data for annual changes in this species (Parker and Brown 1980).

We tracked free-ranging snakes using radiotelemetry. General procedures and equipment used are described by Brown and Parker (1976*a*). Besides providing data on movements and dispersal, transmitters were temperature-sensitive and enabled us to measure deep-core body temperatures of snakes in the field. Each transmitter was calibrated in a water bath against a precision mercury thermometer before and after field use. A 1-min pulse count at each location of a snake in the field was later converted to temperature. We obtained a large number of temperature and microhabitat (location) records of all three species in the field using only those records separated by at least 15 min. Data were discarded when a snake's location or activity could not be ascertained by direct observation or inferred by thermal data. Mean number of records per day for each species were as follows: *Coluber* 2.1, *Masticophis* 3.0, and *Pituophis* 1.7.

Four primary categories of microhabitat or activity were recognized: (1) underground (U), in burrow, including burrows under rocks; (2) under rocks (UR), either surface boulders or rock piles, including hibernacula (snake usually visible); (3) moving (M), actual movement from one place to another; and (4) regulating (R), used here in the sense of thermoregulating.

These categories are recognized for analysis of the spatial dimension of the niche (place niche). The first two (U and UR) are subsurface locations and the last two (M and R) are surface activities. Snakes in concealed positions could be precisely located by disconnecting the antenna and passing the receiver close to the ground surface until a distinctly stronger signal was received. In this manner, a distinction between snakes located under rocks (UR) and underground (U) was possible. Distinction between M and R was, in most instances, based on a visual sighting of the snake. If the snake was not seen but the received signal fluctuated in intensity or faded out, the animal was actively moving. Snakes thermoregulating on the surface (R) sometimes were purposely not observed to avoid disturbing the animal. In such instances the category R was assigned by inference from (1) a high body temperature with respect to shaded ambient air and substrate temperatures and (2) lack of movement. Our R and M categories correspond to the normal activity range and basking categories of Cowles and Bogert (1944), and we use thermal data in these two categories as representing the normal activity temperatures of the snakes.

We designate seasons as follows: spring, April–May; summer, June–August; autumn, September–October. All body temperatures reported in the normal activity range of each species pertain to clear weather conditions (< 60% cloud cover, sun visible).

Our records of food habits were obtained by palpation of live snakes captured between autumn 1969 and autumn 1972 and by examining stomach contents of preserved specimens obtained from the same habitat in areas surrounding the dens. Food items were identified from 146 individuals of the three species (102 *Coluber*, 28 *Masticophis*, 16 *Pituophis*) taken in all months between May and October. Most of the records were from individuals collected in September as they returned to hibernacula. Food items were identified to family or subfamily for insect groups, and to genus or species for vertebrates. Data reported are frequency of occurrence of each food group – proportion of stomachs containing a prey taxon to the total number of stomachs of each species of snake containing food. Although prey biomass would be superior to numbers, digestive fragmentation and small sample sizes (for *Masticophis* and *Pituophis*) would have made the estimation of prey weights from volumes difficult and would have done more to obscure than to reveal interspecific food comparisons. For analysis of the trophic niche dimension, four categories of prey are discerned: insects, lizards, snakes, and mammals.

Using proportions along food and place dimensions actually used by each species, we calculated the niche breadth (B) along any single dimension and species diversity (D) using Simpson's index of diversity (cf. MacArthur 1972)

$$D = B = \frac{1}{\sum_{i=1}^{n} p_i^2} \qquad (1)$$

where p_i represents the proportion of the i^{th} food type or microhabitat used (calculation of B) or the proportion of the total sample belonging to the i^{th} species (calculation of D). B may vary from one to n, the number of p_i values (in our case, 3 for food and 4 for place niches).

To estimate niche overlap, we used a symmetric matrix equation introduced by Pianka (1973) and discussed by May (1975*a*). Our usage of this equation follows that of Pianka (1975) in the sense that it represents niche overlap (O) and is calculated as

$$O_{kj} = \frac{\sum_{i=1}^{n} p_{ij}\, p_{ik}}{\sqrt{\left(\sum_{i=1}^{n} p_{ij}^2\right)\left(\sum_{i=1}^{n} p_{ik}^2\right)}} \qquad (2)$$

where p_{ij} and p_{ik} are the proportions of the i^{th} resource category used by the j^{th} and the k^{th} species respectively. This measure (range 0-1) is calculated from the relative utilization quantities, p_{ij} and p_{ik}, along the food and place dimensions.

Using the Shannon-Wiener equation, we calculated values of species diversity (H) as follows:

$$H = -\sum_{i=1}^{S_T} p_i \ln p_i \qquad (3)$$

where S_T = total number of species in the community and p_i = proportion of the total sample belonging to the i^{th} species. We also calculated maximum species diversity as

$$H_{max} = \ln S_T \qquad (4)$$

and an equitability measure (E) (range 0-1) as the ratio

$$E = \frac{H}{H_{max}} \qquad (5)$$

where H is the observed species diversity according to equation (3). We use equations (3) through (5) to quantify values for several north temperate communities of snakes. We selected certain field studies where both species and numbers of individuals collected by a standard procedure were continued over a fairly long time (usually several months to several years), and where the workers specified their collecting techniques. We have deliberately avoided numerous studies reporting on snakes taken from various winter hibernating locations (cf. Parker and Brown 1973), nor have we treated tropical communities (Inger and Colwell 1977; cf. Henderson et al. 1979). The few censuses and primitive state of our knowledge of the structure of snake communities at present do not allow a comparison of temperate and tropical communities. We believe it is more important to deal with the more fundamental question: What are the relative abundances of sympatric species of snakes?

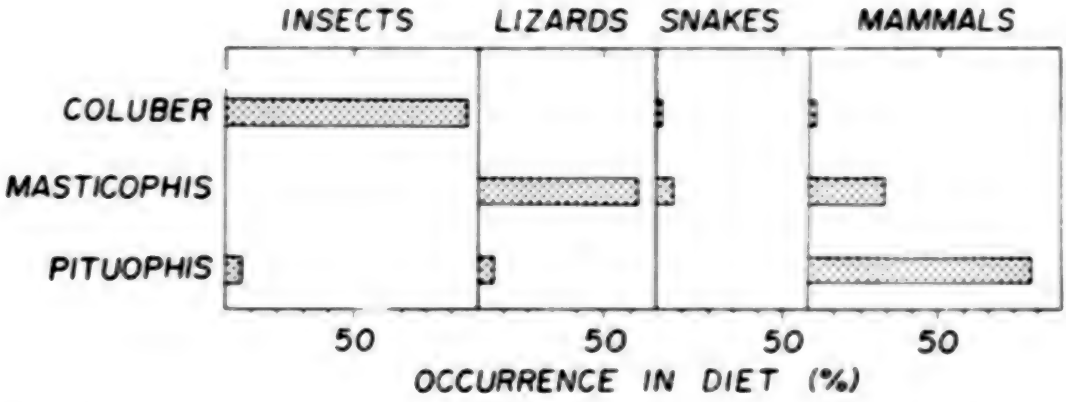

Fig. 1. Frequencies of occurrence (percentage of stomachs) of four major groups of prey taken by three species of colubrid snakes in a Great Basin cold desert shrub habitat in northern Utah

Results

Food Niche

Food habits of the three species of snakes (Fig 1) at our desert study area revealed that each species had eaten three of the four prey groups, and each had a dominant (preferred) prey group taken as follows: (1) *Coluber* (n = 102) were chiefly insectivorous. Most (96%) of the diet consisted of insects (mostly orthopterans: grasshoppers and ground crickets), whereas the remainder consisted of mammals (*Peromyscus*, 3%) and snakes (*Masticophis taeniatus*, 1%). (2) *Masticophis* (n = 28) ate primarily lizards (mainly *Uta stansburiana*, 64%), mammals (mostly *Peromyscus* and *Perognathus*, 28%), and snakes (*Coluber constrictor* and *Masticophis taeniatus*, 7%). (3) *Pituophis* (n = 16) prey consisted largely of mammals (chiefly *Microtus* and *Perognathus*, 87%). Lizards (*Uta stansburiana*, 6%) and insects (Orthoptera, 6%) made up less important items in the diet.

Using the measures B (equation 1) and O (equation 2), we show the trophic niches for each of the three species in Fig. 2. Field data are corroborated by the calculated values showing that *Coluber* has the narrowest food niche (B = 1.08), *Pituophis* is intermediate (B = 1.29), and *Masticophis* has the broadest niche (B = 2.00). Overlap along the food dimension is low between *Coluber* × *Masticophis* (O = 0.013), intermediate between *Coluber* × *Pituophis* (O = 0.102), and high between *Masticophis* × *Pituophis* (O = 0.467) due to the relatively high occurrence of mammals in the diet of each of these species.

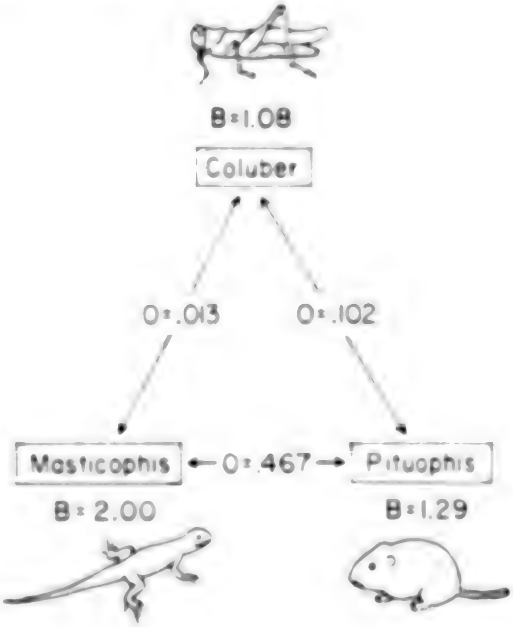

Fig. 2. Quantitative analysis of the food niche of three sympatric colubrid snake species in a Great Basin cold desert shrub habitat. Relations of the three species indicated by niche breadth values (B) at each boxed name and niche overlap values (O) midway along arrows showing comparison of each species pair. Major prey group is depicted for each.

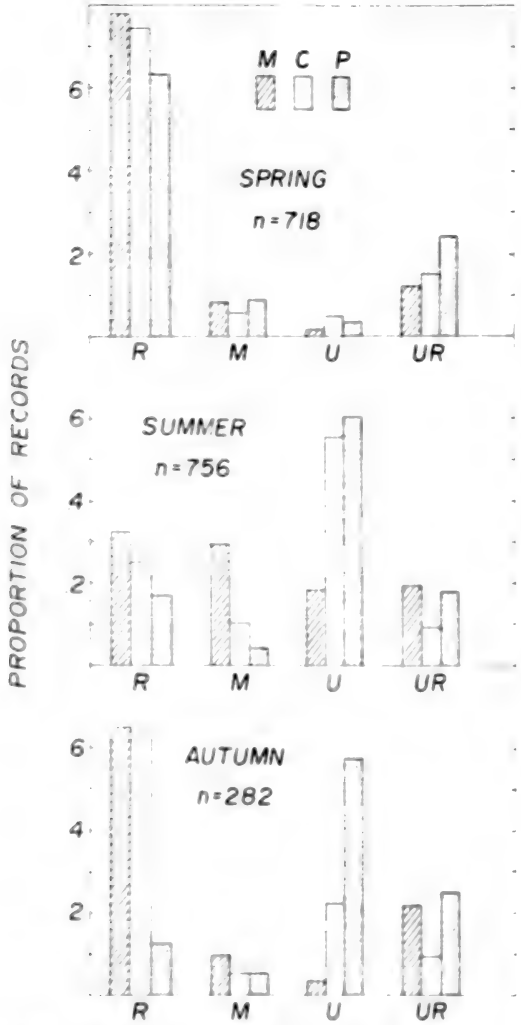

Fig. 3. Seasonal distribution of the place niche of three sympatric colubrid snake species (M = *Masticophis taeniatus*, C = *Coluber constrictor*, P = *Pituophis melanoleucus*) in a Great Basin cold desert shrub habitat. Data are microhabitat-activity categories (R = thermoregulating on surface, M = moving on surface, U = underground, UR = under rocks) recorded for free-ranging snakes in their natural habitat by radiotelemetry in 1971 and 1972. Place niche based on a total of 1,756 field records (*Coluber* 587, *Masticophis* 750, *Pituophis* 419).

Place Niche

Microhabitat – activity distributions (Fig. 3) for the three species in three seasons show several patterns of interspecific spatial-temporal responses: (1) in spring, surface thermoregulation (R) occupied the bulk of the activity of all three species; (2) in summer, most *Coluber* and *Pituophis* retreated underground; and (3) the autumn pattern was like the spring pattern for *Coluber* and *Masticophis*, but not for *Pituophis* (Fig. 3). When activity locations are grouped as to those snakes found R and M or U and UR, two notable spatial niche differences are apparent (Table 1). *Masticophis* in summer tended toward a more uniform (even) dispersion of "places," whereas *Pituophis* failed to reappear on the surface in autumn as did *Coluber*.

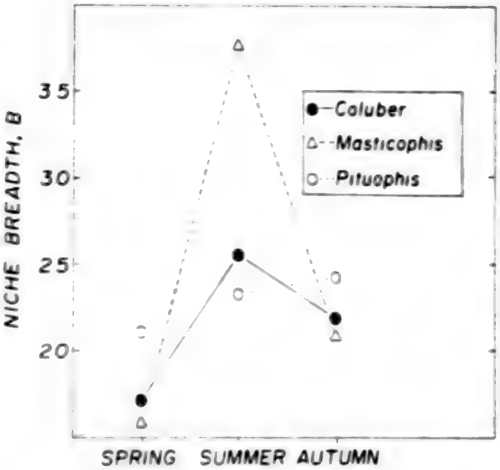

Fig. 4. Seasonal and interspecific comparisons of place niche breadth (B) occupied by three sympatric colubrid snake species in a Great Basin cold desert shrub habitat in northern Utah. Place niche quantified by proportion of location records in four categories of activity-microhabitat used by snakes. See text for calculation of niche breadth and for microhabitat-activity categories recognized.

Niche breadths (B) for the spatial dimension were calculated for each species in the three seasons (Fig. 4). This analysis shows that (1) both *Coluber* and *Masticophis* have narrower place niches than *Pituophis* in both spring and autumn, (2) the place niches of *Coluber* and *Masticophis* are more similar to each other in spring and autumn than either is to *Pituophis*, (3) *Masticophis* has the broadest place niche in summer and differs considerably from both *Coluber* and *Pituophis*, and (4) *Coluber* and *Pituophis* are similar to each other in summer in that they are found underground most often.

Results obtained with place niche overlap computations between the species pairs (Table 2) are as follows: (1) All three paired species

Table 1. *Prominent place niche (activity–microhabitat) locations as surface or subsurface records for three species of colubrid snakes in a cold desert shrub habitat in northern Utah in three seasons, 1971–72*

	Spring		Summer		Autumn	
Species	Location[a]	P[b] (n)	Location	P (n)	Location	P (n)
Coluber (n = 12)	R, M	0.81 (193)	U, UR	0.65 (295)	R, M	0.69 (99)
Masticophis (n = 14)	R, M	0.86 (343)	R, M	0.62 (264)	R, M	0.75 (143)
Pituophis (n = 10)	R, M	0.73 (182)	U, UR	0.79 (197)	U, UR	0.83 (40)

[a] Activity–microhabitat categories: R = thermoregulating on surface, M = moving on surface, U = underground, UR = under rocks.
[b] P = proportions.

comparisons show broad overlap in spring; (2) only *Coluber* × *Pituophis* overlap broadly in summer; and (3) only *Coluber* × *Masticophis* overlap broadly in autumn. Seasonal comparisons of spatial locations show autumn to have lowest overlap values; summer, intermediate place overlap; and spring, highest. Place niche overlap values averaged over all seasons show smallest overall spatial separation of *Coluber* × *Masticophis* and *Coluber* × *Pituophis* and greatest overall spatial separation of *Masticophis* × *Pituophis*.

Thermal Relations

A large number of body temperatures (T_Bs) was obtained by telemetry from snakes monitored in the field (Brown 1973; Parker and Brown 1980). In summer, snakes located U (and therefore largely buffered from solar radiation, wind, and other environmental factors) registered the following T_Bs listed in ascending thermal levels (mean ± 1 SE): *Masticophis* 25.6° ± 0.5° C (17.0 – 30.6, n = 49), *Pituophis* 26.9° ± 0.3° C (15.5 – 31.4, n = 116), and *Coluber* 27.5° ± 0.4° C (17.5 – 35.2, n = 127). Only about 2° C separates body temperatures of the three species underground.

On the surface, we lumped R and M categories to obtain each species' overall activity body temperature. We also include, for comparative purposes, two other snakes and the six sympatric lizard species at our desert study site (Table 3). The lizards as a group had higher mean activity temperatures (34.0° – 37.6° C) than did the snakes (24.3° – 31.8° C). Means of the two groups did not overlap. Among the snakes, *Coluber* and *Masticophis* were the most lizard-like in their normal preferences (31.2 and 31.8° C), whereas *Pituophis* and *Crotalus* T_Bs (27.9° and 28.3° C) were considerably lower. *Masticophis* and *Coluber*, both feeding on highly active and thermally tolerant prey (lizards, grasshoppers), may require high body

Table 2. *Place niche overlap[a] among three sympatric colubrid snakes in a Great Basin cold desert shrub habitat in northern Utah in each of three seasons, 1971–72.*

	Species pair		
Season	*Coluber* × *Masticophis*	*Coluber* × *Pituophis*	*Masticophis* × *Pituophis*
Spring	0.997	0.985	0.978
Summer	0.724	0.976	0.639
Autumn	0.945	0.531	0.363
Mean (all seasons)	0.889	0.831	0.660

[a] See text for equation (2) used to calculate niche overlap values.

Table 3. *Temperatures of active reptiles sympatric at the study location (Great Basin cold desert shrub) in northern Utah.*

Species	No.	Temperature (°C)[a] Mean ± 1 SE	Temperature (°C)[a] Range	Reference
Snakes				
Coluber constrictor	266	31.84 ± 0.20	18.6–37.7	Brown (1973)
Masticophis taeniatus	564	31.21 ± 0.13	14.9–38.4	Parker and Brown (1980)
Pituophis melanoleucus	206	27.87 ± 0.32	12.2–35.0	Parker and Brown (1980)
Crotalus viridis	81	28.32[b]	15.5–35.0	Hirth and King (1969)
Diadophis punctatus	5	24.28	19.8–26.6	Parker and Brown (1974*a*)
Lizards				
Crotaphytus wislizeni	46	36.68 ± 0.32	30.6–41.5	Parker and Pianka (1976)
Phrynosoma douglassi	18	34.88 ± 0.64	26.3–38.8	Pianka and Parker (1975)
Phrynosoma platyrhinos	86	35.46 ± 0.25	28.1–40.5	Pianka and Parker (1975)
Sceloporus graciosus	9	34.01 ± 0.66	30.6–37.7	Parker (1974)
Uta stansburiana	16	35.46 ± 0.54	29.7–37.9	Parker and Pianka (1975)
Cnemidophorus tigris	11	37.64 ± 1.04	29.2–40.8	Parker (1974)

[a] Temperatures for *Coluber*, *Masticophis*, and *Pituophis* are deep-core body temperatures (telemetrically recorded), and for other species, cloacal temperatures (recorded with a Schultheis thermometer).

[b] Estimate from graph.

temperatures to maintain a scope of metabolic activity and behavior sufficient to capture their prey. Jacobson and Whitford (1971) suggested this explanation for the high activity temperature (near 33° C) of the diurnal lizard-eating snake, *Salvadora hexalepis*. In contrast, *Crotalus* and *Pituophis* eat primarily nocturnal or subterranean small mammals, and these snakes are not likely to be active at times when it would be necessary for them to maintain high T_Bs to capture prey. Greenwald (1974) recorded the highest metabolic efficiency (maximal striking speed and successful prey capture) for *Pituophis* at 27° C, virtually identical to the field results obtained telemetrically by Parker and Brown (1980). Although *Coluber* and *Masticophis* share an almost identical range of activity temperatures, they are strongly separated by food habits (see *Food Niche*). *Crotalus* had a mean activity temperature very similar to *Pituophis* and, presumably, rattlesnakes once occupied a mammal-eating trophic niche similar to gopher snakes. *Crotalus* has recently been exterminated (see *Species Composition at Utah Dens*), and now *Pituophis* is the sole occupant of its overall niche as a relatively cool-bodied subterranean mammal predator.

Temporal Overlap at Hibernacula

As all three species move to and from their summer home ranges and their winter denning retreats each year, there is opportunity for interaction or perhaps direct physical contact during the periods of fall ingress and spring emergence. We recorded the temporal sequence of arrival and departure at dens in all seasons, 1969–73 (Brown 1973; Parker 1974). In autumn 1971, for example, three main arrival peaks were clearly evident (Fig. 5): *Masticophis*, mid-September; *Pituophis*, late September; and *Coluber*, early October. *Masticophis* were active on the surface at dens for an average of about 17 days after arrival and many entered hibernation after ecdysis nearby (Parker and Brown 1980). *Coluber* and *Pituophis* were not active at dens after returning, and both species seemingly descended into hibernation immediately upon arrival at a den.

In spring 1971, *Pituophis* and *Masticophis* emerged earliest and together in mid-April, followed by *Coluber* in early May, a difference of some 3 weeks between emergence peaks (Fig. 6). The distinct emergence peaks, in general, correspond to favorable air and soil temperatures for emergence. *Masticophis* males constituted the bulk of the earliest emergers (Parker and Brown 1980), a phenomenon also noted in *Thamnophis sirtalis* and a number of other north-temperate snake species (cf. Gregory 1974). Apparently, differential interspecific emergence is related to enhancement of mating behavior in males of

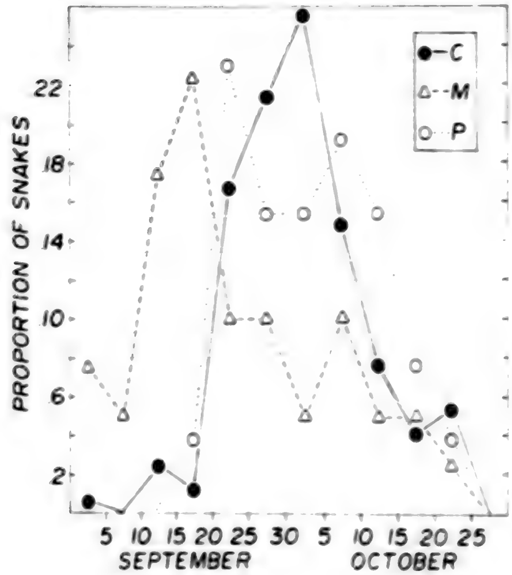

Fig. 5. Arrival of three species of colubrid snakes at den M in autumn 1971. Proportions of each species captured during each 5-day interval are shown. C = *Coluber constrictor*, M = *Masticophis taeniatus*, P = *Pituophis melanoleucus*.

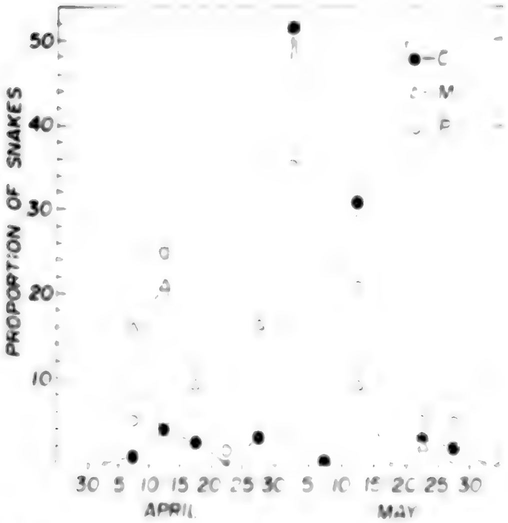

Fig. 6. Emergence of three species of colubrid snakes from den M in spring 1971. Proportions of each species captured during each 5-day interval are shown. C = *Coluber constrictor*, M = *Masticophis taeniatus*, P = *Pituophis melanoleucus*.

some species (e.g., *Masticophis*, Goldberg and Parker 1975; Bennion and Parker 1976) rather than as a mechanism to avoid possible competition, cannibalism, or interspecific predation at the hibernaculum.

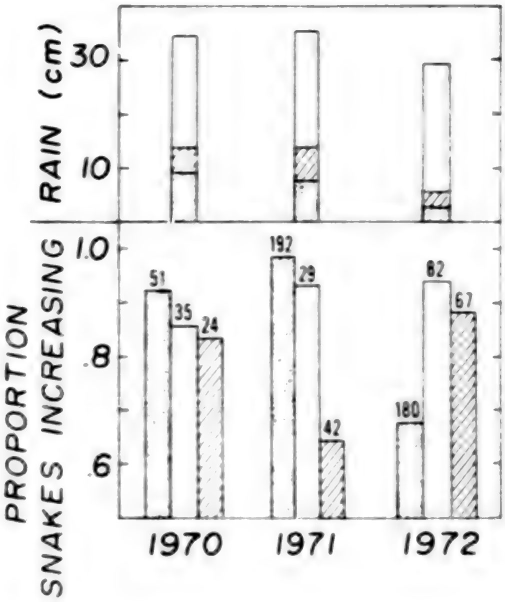

Fig. 7. Annual proportions of three species of colubrid snakes that increased in body weight in 3 successive years (1970-72) in a Great Basin cold desert shrub habitat. Weight change records (lower histogram) are for 423 *Coluber constrictor* of known age through 6 (stippled bars), 146 *Masticophis taeniatus* of all ages (open bars), and 133 *Pituophis melanoleucus* of all ages (hatched bars). Number of records above each bar. Upper histogram shows total annual rainfall (unshaded), total 5-month rainfall (May-September, hatched), and total 3-month rainfall (June-August, stippled) recorded at Grantsville, Tooele County, Utah

Annual Body Weight Changes

We measured weight changes of snakes in each of 3 years (1970, 1971, 1972); a total of 702 individual weight difference records were accumulated for the three species. Proportions of these that showed an increase during the yearly interval appear in Fig. 7. In all 3 years, most (86-94%) *Masticophis* increased, but the responses of *Coluber* and *Pituophis* were not consistent between years except in 1970 when a majority (83-92%) of all three species showed weight gains. In 1971 only 64% of *Pituophis* gained weight (compared with 83% in 1970 and 88% in 1972), and in 1972 only 68% of *Coluber* increased (compared with 92% in 1970 and 98% in 1971). As indicated by these records, (1) all 3 years had uniformly favorable conditions for *Masticophis*, (2) the wet 1971 was unfavor-

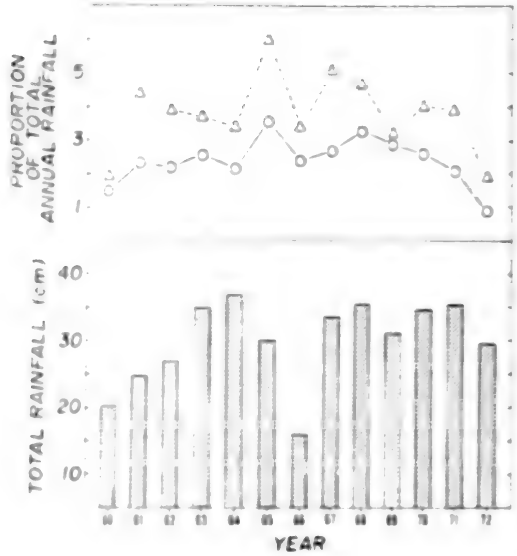

Fig. 8. Rainfall over a 13-year period (1960–72) recorded at Grantsville, Tooele County, Utah (U. S Dep. Commerce, NOAA, Utah Climatological Data). Lower histogram shows total annual precipitation; upper graph shows proportion of total rainfall that fell in the 3-month period June–August (circles) and in the 5-month period May–September (triangles).

able for *Pituophis* and favorable for *Coluber*, and (3) the dry 1972 was a time of growth for *Pituophis* and reduced growth for *Coluber*. The validity of our designations of favorable conditions is reflected in a snake's ability to put on weight and was confirmed by the fact that *Coluber* suffered considerably higher age-specific mortality rates in 1972 than in 1971 (Brown and Parker, 1982).

The striking differential responses of the species were compared with rainfall records at Grantsville, Utah, about 4 km east of the study area. These data show a similar precipitation pattern for 1970 and 1971 (relatively wet years) compared with 1972, a relatively dry year. The 1972 drought showed up markedly during the 3- and 5-month periods of June–August and May–September when snakes are active (Fig. 7). We also plotted total annual precipitation and the proportions of rain that fell during the two periods (Fig. 8). We chose these two periods because they should be critical to a snake's ability to survive (i.e., eat and reproduce) successfully during its short (5 months) activity season. The 13-year total average rainfall was 30.0 ± 1.8 (16.0 – 36.9) cm, of which an average of 38% fell between May and September and 24% fell between June and August. Although 1972 did not receive much less total rainfall than 1970 or 1971, the critical summer periods were very dry, receiving only 19% (May–September) and 9% (June–August) of the year's total.

Species Diversity

From several studies where authors stated the number of species and individuals taken over a fairly long period of time from a specific locality, we computed various species diversity indices from which we attempted to determine what trends or patterns of species abundance, if any, are shown by communities of snakes. The communities we surveyed contained a reported range of species of 3 to 13; Shannon-Wiener functions (H) ranged from 0.592 to 2.151, Simpson's diversity indices (D) from 1.55 to 6.13, and equitability ratios (E) from 0.510 to 0.839 (Table 4). A plot of the Shannon-Wiener values against the logarithm of the number of species in each community (Fig. 9) shows that, with two exceptions, the communities fall roughly along a smooth dome-shaped curve which levels out to an upper asymtotic species number of 12–13.

At our study locality in Utah, a unique opportunity existed for calculation of community variables within a single snake community over a span of about 30 years. Woodbury (1951) earlier worked at den M (one of five major dens in a group of hibernacula called M complex) through 10 years (1940–49). Our sampling was done in the same area over a period of 4 years (1969–73). We previously documented changes in composition of the four common species (three colubrids plus *Crotalus*) during the 30-year interval at this and other dens (Parker and Brown 1973). The changes in relative abundance of these species based on proportions of the total snake fauna at each time (Fig. 10) indicate a major trend for an almost complete replacement of *Crotalus* (54% of total abundance) and *Masticophis* (37%), the two dominant species in the 1940's, by *Coluber* (65%) and *Pituophis* (14%) in the 1970's. Moderate proportions of *Masticophis* (15%) were present along with *Coluber* and *Pituophis* in our sampling period. *Pituophis* increased and *Masticophis* declined since Woodbury's (1951) study.

Table 4. *Species abundance statistics for 10 North American snake communities (cf. Fig. 9). Communities are ranked in order of increasing number of species present. See text for meaning of equations for values calculated and Appendix for species, numbers of individuals, and methods of collection used by each investigator.*

Locality and author	No. species (S_T)	Shannon-Wiener (H)	Simpson's Index (D)	Equitability (E)
Illinois (Seibert and Hagen 1947)	3	0.592	1.55	0.539
Iowa (Klimstra 1958)	5	1.132	2.50	0.704
Maryland (Dargan and Stickel 1949)	5	1.084	2.47	0.674
Utah (Woodbury 1951)	7	0.992	2.34	0.510
Utah (present study)	7	1.051	2.15	0.540
California (Fitch 1949)	9[a]	1.180	2.38	0.568
Louisiana (Tinkle 1957)	10	1.472	3.00	0.639
Arizona (Pough 1966)	12	1.874	4.50	0.754
Arizona (Pough 1966)	12	1.658	3.36	0.667
Arizona (W.S. Parker, unpublished data)	13	2.151	6.13	0.839

[a] Number of individuals not given for one; calculated values pertain to eight species.

A total of eight snake species were tabulated at den M over this time, of which seven were recorded in each study. Among the four rare species, *Diadophis punctatus* and *Rhinocheilus lecontei* were recorded by both Woodbury (1951) and by us. Woodbury caught two *Hypsiglena torquata* and we caught one *Lampropeltis triangulum* as species unique to each study.

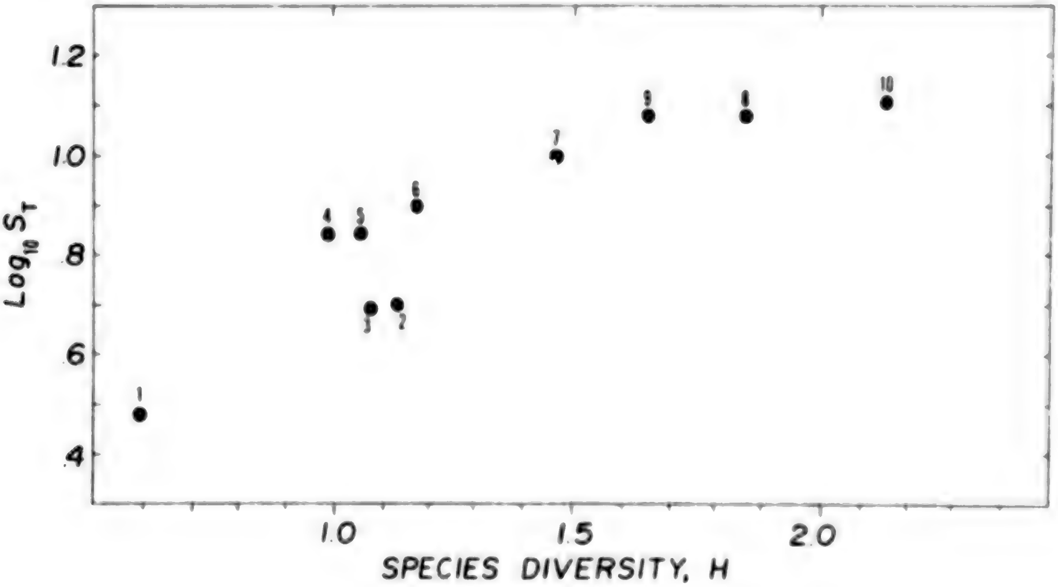

Fig. 9. Species abundance distributions in 10 North American snake communities. Shannon-Wiener diversity index (H) plotted as a function of the logarithm of the total number of species (S_T) in each community. Two communities (4 and 5) are from the same locality in Utah separated by a time span of about 30 years. Values for community 6 based on eight species (cf. Table 4 for values calculated for each community and Appendix for list of species).

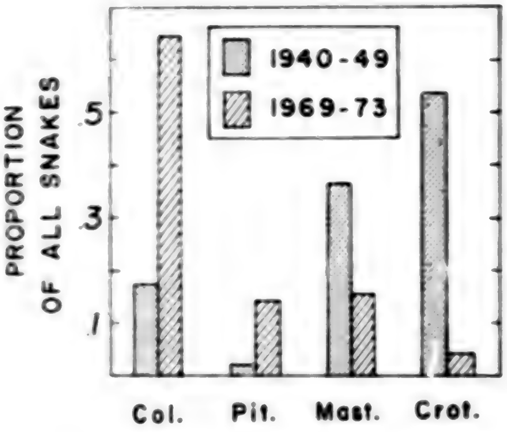

Fig. **10**. Thirty-year changes in relative species abundance of a snake community at a single locality in a Great Basin cold desert shrub habitat in northern Utah. Stippled bars represent data from 1940–49 (community 4, Woodbury 1951), hatched bars data from 1969–73 (community 5; present study). Proportions of each of the four most common snakes (left to right: *Coluber constrictor, Pituophis melanoleucus, Masticophis taeniatus, Crotalus viridis*) are based on total individuals of all species captured at den M in each study. See Appendix for species and numbers of individuals recorded.

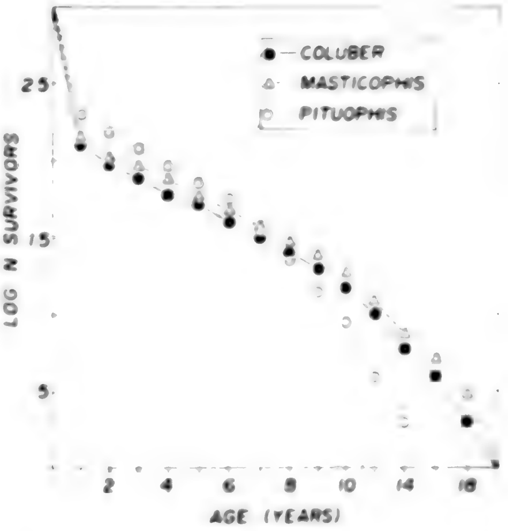

Fig. 11. Survivorship curves for females of three species of colubrid snakes in a Great Basin cold desert shrub habitat in northern Utah. Age-specific annual survival rates obtained empirically by mark-recapture studies in the field. Survivorship data pertain to 1970–72 (Parker and Brown 1980; Brown and Parker 1982).

Survivorship

We measured age-specific survival rates in 1970 and 1971 as an indicator of responses of the populations of *Coluber, Masticophis*, and *Pituophis* to environmental conditions. Details of the demographic aspects of our work, including age-specific growth rates, aging techniques, and fecundity rates are reported elsewhere (Parker and Brown 1980, Brown and Parker, 1982). Here we compare age-specific survivorship curves (Fig. 11). These essentially are similar in the three species, with only minor differences present in first-year (0–1) survival rates (*Coluber* 0.170, *Masticophis* 0.145, *Pituophis* 0.200) indicating generally high mortality among juveniles. Throughout adult life, *Pituophis* had somewhat lower annual survivorship (0.625) than did *Masticophis* (0.800) and *Coluber* (0.787). Some *Masticophis* and *Coluber* survive to a maximum of 20 years, and *Pituophis* to 16 years according to these schedules. Mortality is high in the first-year group, but once individuals attain an age of 1 year, annual mortality is relatively low in all three species.

Discussion

Food Niche

Various studies suggest that the role of food is a dimension of importance in resource partitioning in different communities of sympatric snakes. Carpenter (1952) indicated that differences in food habits of three species of eastern *Thamnophis* were an important factor in their coexistence. He stated that differences in the selection of size and types of prey decreased the competition for food among the three species. Similarly, Fleharty (1967) noted virtually nonoverlapping food preferences among three other species of western *Thamnophis*. Schoener (1974) ranked food type first (over habitat and time of year) as the dimension in which Carpenter's *Thamnophis* were most clearly separated.

Food of snakes is one of the most readily studied aspects of their natural history (e.g., Lagler and Salyer 1945; Fox 1952; Hamilton and Pollack 1956; Brown 1958; Klimstra 1959; White and Kolb 1974) and considerable data have accumulated on their predatory habits. Occupying high positions in the food chains of many communities has also allowed snakes to be sampled for concentrations of environmental pollutants (Fleet et al. 1972; Brisbin et al. 1974; Bauerle et al. 1975). Despite these facts, studies that have attempted to measure the use of trophic resources of more than two sympatric species of snakes are few. Recent approaches to this aspect of assemblages of sympatric snakes (Voris 1972; Mushinsky and Hebrard 1977; Shine 1977; Fitch, this volume; Reynolds and Scott, this volume) indicate that the trophic niche is indeed important to coexisting snakes.

Food clearly seems to represent an important dimension separating two of the three species pairs (*Coluber* × *Masticophis* and *Coluber* × *Pituophis*) in the Utah snake community we studied. Food also is important in resource partitioning among seven common species of snakes in Kansas (Henderson 1974; Fitch, this volume) and, apparently, in a community of seven species in Africa (Barbault 1974) and six species in Australia (Shine 1977).

Feeding responses and innate food preferences are unique aspects of behavioral ecology exhibited by snakes (Burghardt 1970*a*). Possibly, dietary shifts may occur in snakes from communities consisting of a number of potential interspecific competitors. This hypothesis was explored by Carr and Gregory (1976) who tested three species of neonate *Thamnophis* and compared their laboratory response profiles against the natural diets of each, but their results were limited. Still this effort might be pursued in conjunction with analyses of intraspecific geographic variation in the feeding habits of snakes both in the field and in the laboratory. The experimental approach, i.e., demonstration of innate geographic differences in populations within the same species but from different communities (Burghardt 1970*b*; Gove and Burghardt 1975), may yield insights into the complexities of predator-prey interactions in snake communities. Snakes may provide an excellent model vertebrate for testing hypotheses on the contrasting role of inheritance (e.g., Burghardt 1975) versus environment in shaping trophic-dynamic processes in natural communities. Food is very likely an important niche dimension separating snakes in nature. Still, its role is in need of further work.

Place Niche

The early work of Carpenter (1952) on habitat segregation of three sympatric species of *Thamnophis* in Michigan clearly demonstrates the role of this niche dimension in the ecological distribution of snakes. Schoener (1974) considered the place dimension secondary to that of food in separating Carpenter's *Thamnophis* and this interpretation appears to be correct because the major microhabitat categories ("grassy areas," "marsh grass and sedge," "water and water vegetation") were more difficult to define and quantify in the field than were food types. Also, there was considerable overlap in places occupied by these species (cf. Carpenter 1952). Fleharty (1967) used the categories "rocks," "vegetation," and "logs" to classify location preferences among three *Thamnophis* species, and he showed some species differences. The categories of their field recognition appear to us, however, to be inadequate to allow the place dimension to be compared with food.

One recent worker (Hart 1979) has categorized sympatric and allopatric microhabitats as location types of apparent importance to snakes. In allopatry, *Thamnophis sirtalis* in Manitoba, Canada, occurred near marshes and *T. radix* near ponds (Hart 1979). In sympatry, the importance of the habitat to niche discrimination between these species was reduced primarily as a result of a more limited thermal range for activity available to each species. Hart (1979) interpreted this as a behavioral reaction to the thermal limitation rather than as a reaction to the presence of another species.

Other workers have presented analyses of habitat partitioning in a community of closely related snakes (e.g., Pough 1966; Hebrard and Mushinsky 1976; Reynolds and Scott, this volume). Some studies have taken a much larger assemblage of snakes and have subdivided these into broad groups of adaptive zones (aquatic, terrestrial, arboreal, etc.), such as Henderson and Hoevers (1977) in Central America and Leston and Hughes (1968) and Barbault (1971) in Africa. The first two also classified the snake faunas in each tropical region according to activity times (nocturnal, diurnal) and major prey groups taken. Thus, at least two studies have approached snake communities from all three (spatial, temporal, and trophic) fundamental aspects of the niche. These analyses for snakes still provide only preliminary information, however, and data on snakes as a group continue to lag far behind similar approaches to quantify other reptilian communities, especially those of lizards (e.g., Pianka 1973, 1975).

Several related behavioral subdivisions of the place niche of snakes have been partly treated by a number of authors. These aspects seem not to have been emphasized in a parallel way by lizard ecologists, chiefly because they are biological attributes generally of more inconspicuous, secretive, or fossorial animals. They may be summarized briefly as follows: (1) thermal and moisture requirements in habitat selection, especially by small subterrestrial species (Warburg 1964; Clark 1967; Elick and Sealander 1972); (2) communal reproductive (mating and egg-laying) aggregations (Tinkle and Liner 1955; Brodie et al. 1969; Parker and Brown 1972; Aleksiuk and Gregory 1974; Gregory 1975; Palmer and Braswell 1976; Henderson et al. 1980); (3) communal overwintering (hibernation) aggregations (Carpenter 1953; Parker and Brown 1973; Brown et al. 1974); (4) vernal dispersal from and autumnal return to some central place, usually a hibernation den (Hirth et al. 1969; Gregory and Stewart 1975; Brown and Parker 1976*a*); and (5) habitat conditioning and the role of olfaction in orientation (Noble and Clausen 1936; Noble 1937; Dundee and Miller 1968; Burghardt 1970*a*; Gehlbach et al. 1971; Porter and Czaplicki 1974; Ford 1975; Kubie and Halpern 1975).

The above attributes bear on the question, "Where does a snake find itself in space and how is that location affected by other members of its own population?" By tracking snakes carrying radio transmitters and recognizing categories of location or activity, we achieved a method for quantifying the spatial niche of snakes in the field. The telemetric tracking technique also has been used successfully to follow dispersal and home range movements (Brown and Parker 1976*a*; Fitch and Shirer 1971; Parker and Brown 1980). It has high potential for studying other species of snakes in other localities. Its possible adoption by many workers may be limited because it is time-consuming and physically demanding to track more than a few snakes in the field, especially if they are large or are in a migratory phase of activity.

Our computation of niche breadths using the four categories of microhabitat-activity show definite seasonal shifts in all three species. *Coluber*, for example, is a widespread North American snake usually thought of as a diurnal ground-dwelling species. In northern Utah, however, *Coluber* was seldom found above ground during summer. Thus one cannot quantify the place niche of desert snakes in a biologically meaningful way unless the season is specified. A number of authors have examined long-term temporal aspects of snake ecology (Oliver 1947; Seibert and Hagen 1947; Klimstra 1958; Bider 1968; Barbault 1970, 1971; Nelson and Gibbons 1972; Henderson and Hoevers 1977). Patterns of seasonal abundance vary with the locality (especially due to temperate vs. tropical seasonal turnovers in temperature and rainfall) and the component species making up the community. In addition to identifying patterns of partitioning the temporal dimension over long (circannual) time, the question arises as to whether this dimension has any merit at all over short (circadian) time in partitioning this resource in snake communities. Daily time of activity (times of peak abundance since sunrise or sunset) are effective measures for quantifying the time dimension of some lizard niches (Pianka 1973; Creusere and Whitford, this volume), but little is known about snakes. Bider (1968) reported that activity of the diurnal *Thamnophis sirtalis* was bimodal on clear days but unimodal on cloudy days. Hart (1979) noted a shift in the daily activity patterns of *Thamnophis sirtalis* and *T. radix* in sympatry from the patterns present in allopatry. The nocturnal *Trimeresurus flavoviridis* underwent peak unimodal activity between 0100 and 0400 h (Tanaka et al. 1967). Parker and Brown (1980) showed that activity of *Pituophis melanoleucus* was bimodal (morning and afternoon peaks) in summer and unimodal (late afternoon peak) in spring and autumn.

Place Niche Studied by Different Methods

In 1966, A. C. King studied dispersal of snakes from the same den (den M) studied by us and the results of this work (King 1968) were later published (Hirth et al. 1969). The technique used by these workers was to tag snakes with a subdermal radioactive wire and to relocate them during the summer using a scintillo-

Table 5. *Place niche data recorded in 1966 and 1971-72 for two species of colubrid snakes in a Great Basin cold desert shrub habitat. Data are proportions of radioactivity-tagged snakes located in summer 1966 (Hirth et al. 1969) and telemetry-monitored snakes located in summers 1971-72 (Brown 1973; Parker and Brown 1980).*

	On surface		Underground		In shrubs	
Species	1966	1971-72	1966	1971-72	1966	1971-72
Coluber constrictor	0.44	0.35	0.41	0.65	0.15	0
Masticophis taeniatus	0.49	0.62	0.10	0.38	0.41	0

meter. Results of Hirth et al. (1969) on home range biology of *Coluber* were at variance with our results (Brown and Parker 1976a). Hirth et al. (1969) presented data on proportions of *Coluber*, *Masticophis*, and *Crotalus* captured in three strata: underground, on the surface, and in shrubs (Table 5). Differences in proportional utilization for snakes found in surface locations were 0.09 for *Coluber* (higher in 1966) and 0.13 for *Masticophis* (lower in 1966). The most striking contrasts appear in proportions located underground: differences were 0.24 for *Coluber* (lower in 1966) and 0.28 for *Masticophis* (lower in 1966). Hirth et al. (1969) recorded proportions of 0.15 and 0.41 for *Coluber* and *Masticophis* in shrubs, respectively. In contrast, we found no snakes in shrubs.

Did a shift occur in the place niches of these two species during the 5 years intervening between the two studies, or could some other factor(s) be responsible for the different results? We believe that the variance was due to differences in techniques. The study of Hirth et al. (1969) apparently had three major biases. First, the investigators' peak times of searching activity (early morning) coincided with the period during which the snakes' surface activities (basking, moving) were also maximal. Second, these workers could achieve only a 3-m range for detecting a snake located 30 cm underground. Thus, they probably underestimated the frequency of snakes in this location. Third, two workers searched for 64 *Coluber* and 81 *Masticophis* in a 1,000-ha area, and a tagged snake had to be approached to within 9 m for location on the surface; detection thus depended on constant observation of the instrument rather than watching for snakes, so a *Coluber* or *Masticophis* might easily have been flushed into a shrub and then located there. A serious overestimate of snakes located off the ground likely occurred.

Among the large sample of locations (1,756) we recorded, none was an "in shrub" record. We did not observe snakes climbing in shrubs except on a few occasions when they were enclosed inside a fenced den before capture. Snakes we studied were carrying heavier and bulkier objects (constituting 5-10% of a snake's body weight) and this may have behaviorally precluded them from climbing. The snakes we tracked by telemetry, however, appeared to behave as did untagged individuals: their overall activity seemed normal and included migratory movements and home range establishment, thermoregulation and basking, and mating and egg-laying activities (Parker and Brown 1972; Brown 1973; Brown and Parker 1976a). Biases in the technique of Hirth et al. (1969), and perhaps to some extent in our own technique, make the comparative findings on temporal shifts in place niche partitioning difficult to reconcile.

Food and Place Niche Complementarity

As mentioned above, Carpenter (1952) and Schoener (1974) indicated that the food dimension assumes a more important role in separating *Thamnophis* spp. than the place dimension. Other work on snakes seems also to support this notion, particularly as shown by the preponderance of analyses of food habits in the literature as contrasted with a paucity of information on microhabitat segregation within a common space shared by three or more sympatric species. Stomach contents are considerably easier to obtain than spatial use data. In a later analysis, Schoener (1977) ranked macrohabitat (vegetation type) first in separating North American crotalids based on two studies in Arizona. Shine (1977) found only one instance of sympatry between two of six species of elapids in eastern Australia and attributed the low spatial overlap

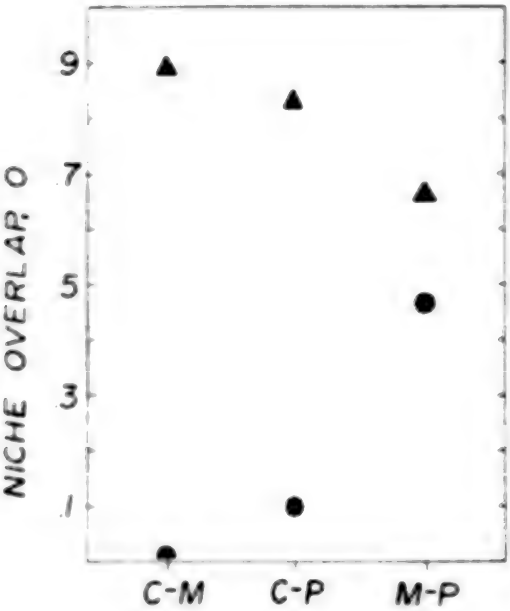

Fig. 12. Niche overlap values along two niche dimensions for each of three species pairs of colubrid snakes (C = *Coluber constrictor*, M = *Masticophis taeniatus*, P = *Pituophis melanoleucus*) in a Great Basin cold desert shrub habitat. Circles show food niche, triangles place niche overlap. Overlap values for place niche are averages of separate values for each of three seasons (cf. Table 2).

to a low diversity of major prey groups with resultant segregation accounted for primarily by dietary differences.

Our results on both niche dimensions (as overlap values for all species pairs) are shown in Fig. 12. First, all three species pairs are more strongly separated along the food dimension (low overlap values) than along the place dimension (high overlap values). Second, high overlap in one dimension corresponds with low overlap in the other. This phenomenon, called "complementarity" by Schoener (1974), was described as follows: "similarity of species along one dimension should imply dissimilarity along another, if resources are to be sufficiently distinct. Such complementarities illustrate especially well the trouble individuals and their genes seem to take to avoid other species' niches . . ." Schoener also documented that the most common instance of complementarity occurs in the food-habitat combination where there is a frequent tendency for species that eat different foods to overlap strongly in habitat. Our data corroborate the occurrence of this in a snake community. The trend is strongest in *Coluber* × *Masticophis* and *Coluber* × *Pituophis* comparisons, and is present but less marked for *Masticophis* × *Pituophis*. For all three paired species comparisons, average overall overlap for place is 0.793 and for food 0.194. This is quantitative evidence for the importance of the food resource over the spatial resource and documents the complementary roles of the trophic and spatial niches in the coexistence of snakes in this particular community.

Annual Body Weight Changes

Several questions arise about the possible factors responsible for the differential interspecific responses of the snakes in years of varying amounts and proportions of summer rainfall. First, why did *Coluber* and *Pituophis* respond in opposite ways in the 2 years of markedly different rainfall patterns (1971 and 1972)? Second, why did *Pituophis* show such different responses in 2 years of virtually identical rainfall patterns (1970 and 1971)? Finally, what factors may have been involved in the very distinct species × year interactions of *Coluber* and *Masticophis*? All queries allude to a possible link between rainfall patterns and the trophic niche of each species and, perhaps, to a direct role of wetness in the habitat and physiological condition of the snakes by affecting their ability to obtain sufficient food or water, or both.

Considering first the possible role of direct effects of water deprivation and integumentary dehydration, *Masticophis* may be a more resistant species (may have lower rates of water loss through the skin) than the other two species. Although no data are available to confirm this hypothesis, Gans et al. (1968) found that desert-adapted species were much more tolerant of desiccation than were mesic-adapted forms (they reported a water loss rate much lower in the terrestrial *Pituophis melanoleucus* than in the aquatic *Nerodia sipedon*). *Masticophis* at our study locality generally occupy an epigean (surface) niche in summer about as often as they do a subterranean one, probably in conjunction with their extensive foraging for lizard prey. This species may be less prone to water loss than either *Coluber* or *Pituophis*. *Pituophis* occupy a subterranean niche in summer and may require higher ambient relative humidities associated with their underground retreats. If this is true, in order to have a deliterious effect on the snakes, extremely dry summers (like that of 1972) would have to result in desiccation of the soil in burrow systems to depths occupied by these snakes (usually less than 50 cm).

Rainfall effects on *Coluber* seem to be more clear-cut than for either of the other species. *Coluber* declined in weight only in the dry year of 1972. This species seems to be more directly dependent on rainfall, which we believe may affect insect populations, the chief prey of *Coluber*. We previously proposed (Parker and Brown 1973) that increasing populations of *Coluber* through the late 1960's and early 1970's may have been influenced by consistent annual rainfall at our study area since 1966 (cf. Fig. 8) and adequate orthopteran insect populations. Grasshopper populations were not censused during this study but they appeared to be less abundant in 1972 than in the 2 earlier years. In 1969 and 1970 these insects were very numerous around the dens. Greater proportions of *Coluber* stomachs contained insect prey (chiefly grasshoppers) in 1969 and 1970 than in 1971 and 1972 (Table 6).

The weight-gain responses of *Pituophis* are an enigma. Seemingly, some small mammals that this species takes were not adversely affected during the dry year (1972) and, if so, *Pituophis* food supplies may have remained ample. Certain seed-eating rodents (*Perognathus*) may be more resistant to unpredictable desert dry spells than the green plant-eating *Microtus* (both species constitute the main prey of *Pituophis*). If so, perhaps *Pituophis* is able to "switch" to the more abundant prey if the prey species are out of synchrony. Whitford (1976) reported asynchronous fluctuations in rodent populations in New Mexico between wet and dry years. Resident heteromyid rodents (*Dipodomys*, *Perognathus*) were reduced in density during a drought and recovered following a period of rainfall after a 10-12 month lag. More mesic-adapted cricetids (*Peromyscus*) responded by immigrating into previously unoccupied habitats and increasing more rapidly than resident species following a wet year (Whitford 1976). More perplexing, however, is the decline in the proportion of *Pituophis* that gained weight in 1971 from 1970 even though both years were nearly identical in total and summer rainfall patterns. Winter and spring rainfall patterns (October-April) also were similar (18.4 cm in 1969-70 compared with 22.6 cm in 1970-71). Lacking census data for small mammals, we can only offer the conjecture that 1970 may have been a favorable year for them (a peak in their population cycles), whereas 1971 may have been a poor year (low populations).

Table 6. *Numbers and proportions of 340* Coluber constrictor *that contained palpable food items in four successive autumn (September-October) sampling periods at den M in Utah.*

Year	No. examined	No. containing food	Proportion containing food
1969	46	23	0.500
1970	23	15	0.652
1971	143	26	0.182
1972	128	11	0.086

In general, the productivity of desert ecosystems is closely dependent on rainfall. Variation in rainfall should differentially influence several taxonomic components of the animal community. This apparently happened with strikingly different effects on the snakes during our study (cf. Parker and Brown 1980, Brown and Parker 1982). Sampling these animals resulted in variable annual population changes, shifting species abundance relationships, and unstable age structures through time.

Species Diversity and Competition

A number of workers have described species diversity and abundance patterns of snakes (Dunn 1949; Dunn and Allendoerfer 1949; Turner 1961; Lloyd et al. 1968; Chanter and Owen 1971; Kiester 1971; Janzen 1976; Rogers 1976). We examined the species abundances of several selected communities of snakes (cf. Fig. 9). These tentatively appear to fit an expected curve for MacArthur's broken-stick distribution as shown by May (1975*b*; his Fig. 5) but the broken-stick and lognormal distributions are indistinguishable for small S_1 values. The assemblages of snakes we have chosen from the literature seem to be ". . . communities comprising a limited number of taxonomically similar species, in competitive contact with each other in a relatively homogeneous habitat

(May 1975b:94). Also, because several workers have been able to classify various assemblages of snakes into feeding guilds (Arnold 1972; Henderson and Hoevers 1977), it would appear plausible that food is the preeminent resource of consequence for snakes. Whether competitive interactions govern their utilization of food resources, however, has not been conclusively demonstrated. Wiens (1977) cautioned against attributing ecological differences between species to competitive exclusion based solely on descriptions of interspecific differences and when experimental demonstrations of competition are lacking. Wiens' critiques are further strengthened in those communities subjected to irregular climatic fluctuations (e.g., extremes in annual rainfall), where continuous competitive interactions seem not to occur. In such variable environments, competition may not be influential in affecting control over species composition (Wiens 1977). Hart (1979) reported a dietary difference between two species of garter snakes (*Thamnophis*) in sympatry but he believed that this reflected a different prey availability in the region of sympatry rather than niche displacement as a result of species interaction. Shine's (1977) demonstration of differences in body size of two species of snakes and in the mean size of their prey in an area of sympatry is consistent, however, with the interpretation that competition between the two snakes produced the observed body size and prey size divergence. In areas of allopatry such divergence did not occur (Shine 1977).

Species Composition at Utah Dens

At our desert study site, we examined the changing species composition and the factors that have influenced this community. The major observations and trends follow.

- *Crotalus* and *Masticophis* declined (nearly to extinction for the former), not because of any large-scale environmental changes, but because of killing by humans (unfortunately, rattlesnakes and whipsnakes have the behavior of remaining visible on the surface in proximity to dens for a time after spring emergence, making them vulnerable to human predators).
- *Coluber* and *Pituophis*, although also remaining largely on the surface in spring, are much more cryptic and retiring, tending not to be conspicuous at all, even to experienced human snake collectors.
- The decline of *Crotalus*, a mammal-eater, may have sufficiently relaxed competition with *Pituophis* for this food resource so that by the late 1960's–early 1970's the *Pituophis* population responded and increased most notably sometime before and during our study.
- The dramatic rise in population sizes of *Coluber* and *Pituophis* between 1950 and 1972 may closely reflect recent changes in the entire community through sustained adequate precipitation levels in most of the years immediately preceding and during our study. There may have been a corresponding stimulation of plant productivity and increasing populations of orthopteran insects and small mammals, the principal prey of these species.

We commented on the last two points previously (Parker and Brown 1973). The observed rapid increase in the *Coluber* population was not sustained through 1972. In that year, which we considered an unfavorable one for *Coluber*, the racer population declined (Brown and Parker 1982).

The snake community in northern Utah has retained a remarkably stable species abundance pattern from Woodbury's time to ours. Despite years of man-caused perturbations to the snake fauna, there is a strong similarity in species diversity and equitability measurements between the two studies ($S_T = 7$; $D = 2.3, 2.2$; $E = 0.51, 0.54$; cf. Table 4). Human predation almost eliminated rattlesnakes and steadily reduced whipsnakes over the years, but was probably minimal in its effects on racers and gopher snakes, which have increased in recent years. The factors we have been able to identify as having produced these shifts in species composition have not created a great long-term change in the several species diversity indices for the community as a whole. They have, rather, resulted in what seem to be fairly orderly replacements of species according to abundances that might be expected if the makeup of this snake community is governed chiefly along a gradient of food resources and secondarily by microhabitat selection. An extirpated species (*Crotalus*) was seemingly replaced by its potential food competitor (*Pituophis*). A reduced species (*Masticophis*) and an increasing species (*Coluber*) may have had little direct influence on each other or on *Crotalus* and *Pituophis*. All three colubrids were differentially affected by climatic conditions. *Coluber*, and perhaps *Pituophis*, apparently were most strongly influenced by rainfall.

The Fate of the Dens

We have stated that rattlesnakes (*Crotalus*) and whipsnakes (*Masticophis*) are easy targets for certain unprincipled humans to kill. More than all other factors, man has been the main cause for the disappearance of these two species from the den M population. An additional factor is fire. On 17 June 1974 an extensive range fire completely razed a large area which included all of the dens. This fire, by destroying the habitat of an area that more than encompasses the dispersal range of the snakes (a several kilometer radius around the dens), virtually assures the extinction of *Crotalus* (cf. Parker and Brown 1974*b*). Even if many snakes (mostly *Coluber* and *Pituophis*) had managed to survive the blaze by being underground as it swept through, their chances of survival for the remaining 2.5 months of summer 1974 would have been greatly reduced. Beyond this, by autumn 1974 windblown sand had begun to fill crevices between the rocks of the dens (A. C. King, personal communication). W. S. Brown revisited the dens briefly on 6 August 1976. Except for small parts of the largest rocks of dens M and 2 which were still protruding, all other dens of M complex were almost totally buried by sand and were hardly recognizable from the surrounding terrain. The communal hibernacula appeared to be permanently altered and probably now are destroyed for any future occupancy by snakes.

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Appendix

Species and numbers of individuals of snakes from community samples analyzed in text (cf. Table 4, Fig. 9).

1. Illinois (Seibert and Hagen 1947 – hand captures): *Thamnophis radix* 298, *Opheodrys vernalis* 78, *Thamnophis sirtalis* 7.
2. Iowa (Klimstra 1958 – observations, hand captures): *Coluber constrictor* 475, *Elaphe obsoleta* 233, *Heterodon platyrhinos* 78, *Natrix sipedon* 50, *Thamnophis sirtalis* 14.
3. Maryland (Dargan and Stickel 1949 – wire traps): *Heterodon platyrhinos* 36, *Coluber constrictor* 22, *Elaphe obsoleta* 6, *Thamnophis sirtalis* 2, *Lampropeltis getulus* 1.
4. Utah (Woodbury 1951 – hand captures, den fence): *Crotalus viridis* 930, *Masticophis taeniatus* 632, *Coluber constrictor* 127, *Pituophis melanoleucus* 36, *Hypsiglena torquata* 2, *Diadophis punctatus* 2, *Rhinocheilus lecontei* 1.
5. Utah (Brown and Parker 1969-1973 – den M fence; all dens in parentheses): *Coluber constrictor* 332 (1,045), *Masticophis taeniatus* 79 (223), *Pituophis melanoleucus* 74 (144), *Crotalus viridis* 21 (22), *Diadophis punctatus* 5 (7), *Lampropeltis triangulum* 1 (3), *Rhinocheilus lecontei* 1 (1).
6. California (Fitch 1949 – hand captures): *Crotalus viridis* 679, *Pituophis melanoleucus* 256, *Thamnophis elegans* 97, *Lampropeltis getulus* 43, *Masticophis lateralis* 26, *Thamnophis sirtalis* 24, *Rhinocheilus lecontei* 4, *Diadophis punctatus* 2, *Hypsiglena torquata* (number of individuals not reported).
7. Louisiana (Tinkle 1957 – hand captures): *Thamnophis proximus* 221, *Agkistrodon piscivorus* 73, *Natrix sipedon* 60, *Natrix cyclopion* 18, *Lampropeltis getulus* 18, *Coluber constrictor* 16, *Farancia abacura* 5, *Elaphe obsoleta* 4, *Opheodrys aestivus* 3, *Natrix rigida* 2.
8. Arizona, San Simon and San Bernardino Valleys (Pough 1966 – nocturnal road captures): *Crotalus scutulatus* 67, *Pituophis melanoleucus* 28, *Crotalus atrox* 23, *Ari-*

zona elegans 16, *Lampropeltis getulus* 8, *Rhinocheilus lecontei* 8, *Salvadora hexalepis* 6, *Thamnophis marcianus* 3, *Trimorphodon lambda* 3, *Hypsiglena torquata* 3, *Heterodon nasicus* 2, *Ficimia cana* 1.

9. Arizona, Portal Road (Pough 1966 – nocturnal road captures): *Crotalus scutulatus* 58, *Crotalus atrox* 19, *Pituophis melanoleucus* 11, *Arizona elegans* 9, *Crotalus molossus* 7, *Rhinocheilus lecontei* 4, *Salvadora hexalepis* 2, *Trimorphodon lambda* 2, *Hysiglena torquata* 1, *Elaphe triapis* 1, *Thamnophis cyrtopsis* 1, *Heterodon nasicus* 1.

10. Arizona, Phoenix South Mountain Park (Parker, unpublished data, 1964-66 – subsurface can traps, D.O.R.): *Leptotyphlops humilis* 20, *Masticophis flagellum* 7, *Salvadora hexalepis* 6, *Hypsiglena torquata* 5, *Pituophis melanoleucus* 5, *Chilomeniscus cinctus* 5, *Crotalus mitchelli* 4, *Crotalus atrox* 2, *Crotalus cerastes* 2, *Crotalus scutulatus* 1, *Masticophis bilineatus* 1, *Phyllorhynchus decurtatus* 1, *Chionactis occipitalis* 1.

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Resources of a Snake Community in Prairie–Woodland Habitat of Northeastern Kansas

by

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Abstract

In a 30-year study of a snake community at the University of Kansas Natural History Reservation, 22,093 snakes of 12 species were captured 26,346 times, and 2,360 food items were identified. The smallest species, *Diadophis punctatus*, was by far the most abundant, and its biomass was more than twice those of all other species combined. Like the two other small and abundant species, it was almost exclusively an earthworm-eater, and earthworms constituted 70% of the food biomass of all species combined. Every species overlapped several others in the composition of its food, but no two were just alike. Besides earthworms, the most abundant local species of small vertebrates made up most of the food, especially *Microtus ochrogaster*, *Sylvilagus floridanus*, *Peromyscus leucopus*, and *Rana blairi*. Each of these was important in the food of several species of snakes. Intraspecific partitioning of prey species was much more prominent in some snakes than in others. In *Agkistrodon contortrix* the first-year young and adults used different kinds of prey with little or no overlapping, and less complete partitioning between young and adults was evident in all but the earthworm-eaters. Also, some partitioning of prey species was evident between male and female, at least in *Agkistrodon contortrix*, *Coluber constrictor*, and *Thamnophis sirtalis*, in each of which one sex grows to be markedly larger than the other.

A recent trend in the study of ecology has been the detailed analysis of one taxonomic group within a biotic community, such as mammals (Rosenzweig and Sterner 1970; Brown and Lieberman 1973; Heithaus et al. 1975); birds (Cody 1974); lizards (Pianka 1973); frogs (Crump 1974); salamanders (Fraser 1976); or fish (Keast 1965) to determine how their component species coexist. Snakes are relatively difficult subjects for such investigations because of their secretive habits; consequently, little progress has been made in studying them. Unusual opportunity to gain insight into the functioning of a snake community has been afforded me as resident naturalist over 30 consecutive seasons on the University of Kansas Natural History Reservation, where 16 species of snakes are known to occur. During the 30-year interval, the entire biotic community, including its snake component, was progressively altered by ecological succession. Also, the amount of field effort changed, as did field procedures and techniques. Nevertheless, the 30 years of records provide some basis for comparing populations of all the species, in local distribution, composition, density, stability, and impact on the community as a whole. The present account is concerned primarily with food habits and the partitioning of food resources among the 12 most common species. Henderson (1974) has already presented a brief preliminary account of resource partitioning among the snake species of the Reservation, as indicated by autecological accounts of several of them (Fitch 1960, 1963*a*, 1963*b*, 1965, 1975; Clark 1970; Fitch and Fleet 1970). Other types of snake communities are discussed by Brown and Parker, Lillywhite, and Reynolds and Scott in the present volume.

Methods and Materials

Snakes were captured by hand, in wire funnel traps, or beneath sheltering objects – strips of sheet metal, boards and flat rocks – strategically placed to attract them. Routine processing included sexing, measuring, weighing, and palping up undigested food items from the stomach. Fecal material voided by those in traps, or those handled, was saved for study beneath a dissecting microscope for identification of prey items.

Field work began on the newly created 239-ha University of Kansas Natural History Reservation in the northeastern corner of Douglas County in July 1948, and continued through October 1977. Although much of this field effort was concentrated on a series of autecological studies of the commonest species, every available snake, regardless of species, was captured, examined, and processed (Table 1). Individual marking of *Diadophis punctatus* and *Carphophis vermis* was discontinued in 1969 but marking of the remaining species continued to the present (1977). Data published in a series of papers (Fitch 1960, 1963*a*, 1963*b*, 1965, 1975; Clark 1970; Fitch and Fleet 1970) were freely used in combination with records more recently accumulated as a basis for the present report.

Results

Habitat

The University of Kansas Natural History Reservation comprising the study area was a changing mosaic of diverse habitats during the years spanned by the study. Plant communities were mixtures of eastern deciduous forest species including climax oaks and hickories, tallgrass prairie species, and weedy species characteristic of disturbed, seral communities. At the outset about half the area was second-growth woodland dominated by large American elms (*Ulmus americana*), and the remainder was open land that had been used for grazing or for growing corn and other cultivated crops. During the 30-year interval, shrub and tree species invaded the open areas, with ever-expanding thickets, first originating along edges and gullies, and later from secondary foci in the fields.

The woodland areas were far more stable than the areas that were originally open fields. However, changes occurred in the density and composition of the forest: (1) most large elms died from phloem necrosis, breaking the continuity of the foliage canopy and causing a thickening of the undergrowth; (2) parts of the wood-

Table 1. *Twelve species of snakes of the University of Kansas Natural History Reservation arranged according to total number of captures over a 30-year period, with total numbers of individuals captured and body weights.*

Species	Total number of captures	Total individuals	Adult weights Mean (g)	Adult weights Maximum (g)	Mean and range of weights of hatchlings or neonates (g)	
Diadophis punctatus	16,509	14,759	4.0	15.2	0.8	(0.6–1.6 in 43)
Agkistrodon contortrix	3,451	2,681	108.0	400.0	11.4	(7.6–17.0 in 63)
Coluber constrictor	2,376	1,414	126.0	538.0	4.2	(2.4–5.8 in 76)
Thamnophis sirtalis	1,938	1,569	68.0	410.0	1.9	(0.7–2.3 in 39)
Elaphe obsoleta	695	502	253.0	1,020.0	11.7	(7.5–14.7 in 34)
Carphophis vermis	276	255	6.4	14.5	1.2	
Nerodia sipedon	271	206	207.0	480.0	5.0	(3.6–6.8 in 37)
Lampropeltis calligaster	207	166	164.0	405.0	7.5	(6.0–8.0 in 6)
Pituophis melanoleucus	194	161	613.0	1,475.0	25.0	(12.0–34.1 in 20)
Storeria dekayi	186	183	4.5	12.1	0.3	(0.2–0.5 in 73)
Lampropeltis triangulum	134	106	50.0	105.0	2.8	(2.5–3.0 in 5)
Crotalus horridus	109	91	520.0	2,386.0	19.0	(23.0–46.0 in 19)
Total	26,346	22,093				

land that had been grazed before 1948 were relatively open at first, but dense undergrowth developed within a few years after livestock were removed; and (3) the general trend toward a forest climax proceeded, with trees growing larger, natural thinning taking place, and underbrush becoming sparser as the maturing trees developed a denser and more continuous leaf canopy.

Because of the interdigitating and overlapping of habitats, any of the 12 snake species studied might be found anywhere on the area. Seasonal shifts and dispersal of individuals resulted in syntopic occurrences of different species that ordinarily are separated. Each species is somewhat different from all others in its preference and range of habitats.

Agkistrodon contortrix. – Open, rocky woodland, woodland edge, and meadows with clumps of brush adjacent to woodland. Adult males wander farthest from the forest; adult females, especially nonbreeders, also move into meadows; but first-year young remain in the forest. The whole population returns to wooded hilltop rock outcrops of southern exposure to find hibernacula.

Carphophis vermis. – Chiefly in edge of woodland, especially where undergrowth is sparse and soil is loose and damp; flat rocks are used for shelter.

Coluber constrictor. – High grass and mixtures of grass and weedy vegetation or brush. In autumn most of the snakes move into woodland in search of hibernacula in rocky outcrops.

Crotalus horridus. – Deciduous forest, especially of open type, with dry, rocky areas and rugged terrain.

Diadophis punctatus. – Both forest and prairie, but especially along woodland-grassland border in situations providing abundant surface cover and sunshine. Highest densities are observed in open type of woodland on rock-strewn south-facing slope.

Elaphe obsoleta. – Woodland, especially that of open type with dry rocky areas and rugged terrain, but also in adjacent meadow and brushland; they have some affinity for edificarian situations.

Lampropeltis calligaster. – Grassland, including tallgrass prairie, grazed pasture, and meadow with brush clumps.

Lampropeltis triangulum. – Woodland glades and woodland edge where sunshine and shade are available and ground cover, such as flat rocks, is abundant.

Nerodia sipedon. – Ponds and streams, occasionally wandering into adjacent woodland or meadow. In autumn they abandon aquatic habitats to traverse woodland areas seeking hilltop rock-fissure hibernacula.

Pituophis melanoleucus. – Tallgrass prairie and brushy meadow but more numerous on cultivated land or grazed pasture. Those caught on the Reservation were mostly stragglers or transients passing between summer ranges and hilltop rock-fissure hibernacula.

Storeria dekayi. – Woodland edge and brushy meadow, often in damp situations.

Thamnophis sirtalis. – Brushy meadow and woodland edge, with strong affinity for water in ponds, streams, marshes, or temporary puddles.

Population Density

All species included in this study are on fixed annual schedules that entail breeding after spring emergence, embryonic development extending through much of the growing season, and an annual cohort of hatchlings or neonates appearing in late summer or early autumn. Hence there is an annual cycle in numbers, from a maximum in autumn to a minimum just before the next cohort of young is added.

Other population changes are controlled by ecological succession. At the beginning of my field study, the Natural History Reservation had only recently been placed under protection as a natural area. It had been subjected to various uses, including cultivation, grazing of large blocks, and tree-cutting on wooded slopes. After cessation of these activities, secondary succession was extremely rapid at first, becoming much slower in the later years of field work.

Techniques for accurately censusing snake populations have not been established. Because of the generally secretive habits of snakes, direct counts cannot be made except under unusual circumstances. Attempts to census by capture-recapture ratios have usually been unsatisfactory, because the theoretical assumptions necessary cannot be met. Table 2 presents selected figures for population densities of five common species, based on capture-recapture data for the years when sampling by livetrapping was most intensive. In each instance, the samples used ex-

Table 2 *Population densities of six species of common snakes as revealed by capture-recapture ratios of marked individuals on the University of Kansas Natural History Reservation.*

Species	Mean number and range per ha	Number of censuses	Size of sampled area (ha)	Years of sampling	Source
Agkistrodon contortrix	7.4 (6.3–8.5)	2	46	1958–59	Fitch 1960
Coluber constrictor	4.7 (0.9–14.6)	37	16 and 55.5	1955–61	Fitch 1963*a*
Diadophis punctatus	1,266 (719–1,808)	7	3.8 and 5.8	1966–67; 1969–70	Fitch 1975
Elaphe obsoleta	0.9	1	101	1958	Fitch 1963*b*
Thamnophis sirtalis	3.7 (2.0–7.3)	6	71, 137, 151	1958–63	Fitch 1965

excluded first-year young, and the data were limited to areas of favorable habitat where sampling by trapping was considered to be most effective. The traps were not set in any geometrical pattern, but were positioned to take advantage of natural features, such as field edges, gullies, and rock outcrops, and to use available shade. Trapping for the larger species was most intensive from 1957 through 1963, and figures obtained represent population levels within that period.

The extremely high population figure indicated for *Diadophis punctatus* is more than 170 times as abundant as the next commonest species (Table 2). The suggestion that 1,266 *Diadophis* per hectare be accepted as a representative density may elicit skepticism, but supporting evidence has been assembled in an earlier report (Fitch 1975). The samples seemed adequately large, the study area was enclosed by less favorable habitats or partial barriers preventing large-scale interchange with nonresident populations, and extensive trailing of individuals equipped with radioactive tantalum tags showed that they remained on the study area for long periods (R. L. Lattis, personal communication). Large daily samples (as many as 279 snakes) always contained some that were marked, but these never made up more than a small percentage of the catch. It was evident that the many hundreds marked each season constituted only a small part of the pool of resident snakes.

Changes in population levels are normal responses to climatic trends and ecological succession. However, intensive resampling in 1977 showed that essentially the same group of species was present as in 1948, and relative abundances had not drastically changed in most instances. One exception was that of *Tantilla gracilis*. It was confined to two small areas of rocky, xeric habitat in 1950, and not found after 1955; seemingly it was eliminated by successional habitat changes. Records of *Crotalus horridus* dwindled from 53 in the first decade of field work to 39 in the second decade and only 1 in the third. Succession in the forest, which closed the canopy and enveloped clearings by trees and brush, deteriorated the rattlesnake's habitat. Also, a rapidly growing human population in the general neighborhood and escalated traffic on a county road through the area and along its boundary, contributed to the great reduction in number of rattlesnakes, which, according to the testimony of long-time residents, were abundant in the early 1900's. *Lampropeltis getulus*, *Elaphe guttata*, and *Virginia valeriae* have been recorded only a few times and, with *T. gracilis*, are omitted from this discussion.

For seven species (*Carphophis vermis*, *Crotalus horridus*, *Lampropeltis calligaster*, *L. triangulum*, *Nerodia sipedon*, *Pituophis melanoleucus*, and *Storeria dekayi*) records were so meager and sporadic that they were inadequate for capture-recapture censuses by Petersen indices. A population estimate for each was obtained by comparing the numbers captured over a period of months or years with those of a commoner species of somewhat similar habits and local distribution (Table 3). It may be assumed that the species compared are, in every instance, somewhat different in their ecology and "catchability"; hence the population estimates indicate orders of magnitude, but cannot be considered highly accurate.

Carphophis vermis, having an estimated density of 23/ha, is much more abundant than any of the other six species (Table 3). The figure is based on the ratio of 26 *Carphophis* to 1,437 *Diadophis* trapped over the 3-year period (1965–67), on the same area where *Diadophis* was censused by Petersen Index at 1,266/ha. In 1966 and 1967 on a 0.47-ha study area of rocky wooded pastureland on a farm near the northwest corner of the Reservation, Clark (1970) censused *C. vermis* on the basis of capture:recapture ratios. His estimate was 480 snakes per ha in 1966, and 292/ha in 1967 (a "bad" year when the earthworm prey was relatively scarce and unavailable because of drought). In similar habitat of rocky, open woodland on a south slope of the Reservation in 1957, a ratio of 40 *Carphophis* to 188 *Diadophis* was obtained; that ratio would indicate a density of 269 *Carphophis* per ha if the *Diadophis* density was the same there as on the part of the Reservation where it was censused by Petersen Index. This assumption seemed plausible Although the figures from Clark's area and the 1957 sample on the Reservation indicate that in optimum habitat *C. vermis* may attain densities exceeding 200/ha, these figures are much too high to represent extensive areas. Support for the figure of about 23/ha is found in the *Carphophis* to *Diadophis* ratio of 255 to 14,759 in the 30-year totals, indicating a density of 22 *Carphophis* per ha.

Kinds of Prey and Frequencies of Occurrence

The composite of food items (Table 4) was assembled from data collected over many years by direct observation, palped stomach items, and scat residues identified microscopically. As such, they are subject to various biases. The prey identified from stomachs and that from scats showed somewhat different trends, partly because some kinds of prey are digested much more rapidly and more completely than others. Also, as brought out in a later section, there are different trends between young and adults, and even between the sexes. Season and stage of succession may cause other differences.

Most prey items were determined to species, but some were determined only to genus or family, or even broader categories such as "bird" or "reptile." In Table 5 the list of prey has been shortened by lumping some categories; for instance the occasional occurrence of *Microtus* sp. and *Peromyscus* sp. has been combined with the commonest local species, *Microtus ochrogaster* and *Peromyscus leucopus*, respectively.

Table 3. *Estimated densities of uncommon or secretive species based on comparison with associated species censused by capture-recapture ratios.*

Species samples	Years of sampling	Commoner species compared	Ratio to commoner species	Density of commoner species (no. per ha)	Estimated density (no. per ha)
Carphophis vermis	1965–67	*Diadophis punctatus*	26 to 1,437 (1.81%)	1,266.00	22.9
Crotalus horridus	1956–57,	*Coluber constrictor*	40 to 615 (6.50%)	4.72	0.306
	1959–61				0.322
Lampropeltis calligaster	1957–61	*C. constrictor*	42 to 615 (6.82%)	4.72	0.139
L. triangulum	1957–61	*Thamnophis sirtalis*	17 to 457 (3.72%)	3.74	0.237
Nerodia sipedon	1957–61	*T. sirtalis*	29 to 457 (6.35%)	3.74	0.131
Pituophis melanoleucus	1957–61	*Coluber constrictor*	17 to 615 (2.77%)	4.72	15.7
Storeria dekayi	1966–67	*Diadophis punctatus*	183 to 14,759 (1.24%)	1,266.00	

Table 4. *Food items taken by 11 snake species, Natural History Reservation, Lawrence, Kansas (n = total number of food items).*

Species	No. of food items	Species	No. of food items
Agkistrodon contortrix, n = 602			
Microtus ochrogaster	116	*Carphophis vermis*	6
Tibicen pruinosa	93	*Mus musculus*	5
Peromyscus sp	81	*Scincella lateralis*	3
Diadophis punctatus	45	*Thamnophis sirtalis*	3
Blarina brevicauda	42	*Coluber constrictor*	3
Cryptotis parva	35	Birds	2
Caterpillars	34	*Neotoma floridana*	2
Eumeces fasciatus	30	*Sylvilagus floridanus*	2
Pitymys pinetorum	26	*Synaptomys cooperi*	2
Reithrodontomys megalotis	19	*Terrapene ornata*	1
Gastrophryne olivacea	13	*Eumeces obsoletus*	1
Rana blairi	12	*Cnemidophorus sexlineatus*	1
Ophisaurus attenuatus	8	*Elaphe obsoleta*	1
Zapus hudsonius	7	Snakes	1
Sigmodon hispidus	7	*Pseudacris triseriata*	1
Carphophis vermis, n = 50			
Earthworms (*Allolobophora trapezoides* and other species, Clark 1970)			50
Coluber constrictor, n = 986			
Insects			
Acheta assimilis	144	*Spharagemon equale*	7
Ceuthophilus maculatus	97	*Syrbula admirabilis*	6
Arphia simplex	73	*Conocephalus* sp	6
Melanoplus bivittatus	71	*Tibicen* sp	5
M. femurrubrum	68	*Mocris* sp	5
Insects	45	Katydids	4
Acheta sp	44	*Orchelimum* sp.	4
Melanoplus differentialis	43	*Amblycorypha inastera*	2
Neoconocephalus robustus	38	*Melanoplus scudderi*	2
Unspecified beetles	17	*Schistocerca obscura*	2
Melanoplus sp	17	*S. americana*	1
Dissosteira carolina	16	*Neoconocephalus* sp	1
Orchelimum vulgare	15	*Dahinia brevipes*	1
O. nigripes	9	*Tibicen pruinosa*	1
Chortophaga viridifasciata	9	*T. lyrica*	1
Vertebrates			
Microtus ochrogaster	80	*Blarina brevicauda*	3
Peromyscus leucopus	20	*Eumeces obsoletus*	3
Thamnophis sirtalis	17	Reptiles	3
Coluber constrictor	16	Bird eggs	3
Diadophis punctatus	15	*Peromyscus maniculatus*	2
Peromyscus sp	14	*Scalopus aquaticus*	2
Microtus sp	9	*Sylvilagus floridanus*	2
Reithrodontomys sp	8	*Cnemidophorus sexlineatus*	2
Cryptotis parva	7	*Pitymys pinetorum*	1
Eumeces fasciatus	5	Shrews	1
Birds	5	*Nerodia sipedon*	1
Rana blairi	4	*Ophisaurus attenuatus*	1
Sigmodon hispidus	4	*Gastrophryne olivacea*	1
Elaphe obsoleta	4	*Hyla chrysoscelis*	1

Table 4. Continued

Species	No. of food items	Species	No. of food items
Lampropeltis calligaster, n = 56			
Microtus sp.	15	*Coluber constrictor*	1
M. ochrogaster	8	*Ophisaurus attenuatus*	1
Pitymys pinetorum	2	*Synaptomys cooperi*	1
Scalopus aquaticus	5	*Mus musculus*	1
Peromyscus sp.	3	*Sigmodon hispidus*	1
Cryptotis parva	2	*Blarina brevicauda*	1
Colinus virginianus (eggs)	2	*Sylvilagus floridanus*	1
Colinus virginianus	9	*Diadophis punctatus*	1
Eumeces fasciatus	2		
Lampropeltis triangulum, n = 21			
Eumeces fasciatus	12	*Peromyscus maniculatus*	1
Cryptotis parva	4	*Carphophis vermis*	1
Diadophis punctatus	2	*Eumeces obsoletus*	1
Nerodia sipedon, n = 9			
Rana catesbeiana	5	*Acris crepitans*	1
R. blairi	2	*Bufo americanus*	1
Pituophis melanoleucus, n = 18			
Peromyscus (*leucopus* and perhaps *maniculatus*)	2	Birds	4
Neotoma floridana	2	*Pitymys pinetorum*	1
Bird eggs	2	*Sigmodon hispidus*	1
Microtus ochrogaster	4	*Sylvilagus floridanus*	1
		Mus musculus	1
Crotalus horridus, n = 28			
Sylvilagus floridanus	7	*S. niger*	1
Microtus ochrogaster	4	*Sigmodon hispidus*	1
Pitymys pinetorum	4	*Zapus hudsonius*	1
Peromyscus leucopus	3	*Mus musculus*	1
Neotoma floridana	3	*Cryptotis parva*	1
Sciurus carolinensis	1	*Coluber constrictor*	1
Diadophis punctatus, n = 229			
Earthworms	221	Tipulid larvae	7
		Ophisaurus attenuatus	1
Elaphe obsoleta, n = 100			
Microtus ochrogaster	25	Bird nestlings	3
Peromyscus leucopus	19	*Reithrodontomys megalotis*	2
Bird eggs	11	*Blarina brevicauda*	2
Ranid frogs	8	*Neotoma floridana*	2
Sylvilagus floridanus	8	*Eumeces fasciatus*	2
Cyanocitta cristata	6	*Zapus hudsonius*	1
Mammals	5	*Mus musculus*	1
Cardinalis cardinalis nestlings	4	*Sayornis phoebe*	1
Thamnophis sirtalis, n = 72			
Rana blairi	25	*Rana catesbeiana*	4
Bufo americanus	10	*Peromyscus leucopus*	3
Lumbricid earthworms	8	Frogs	3
Hyla chrysoscelis	7	*Microtus ochrogaster*	2
Bufo woodhousei	4	*Reithrodontomys megalotis*	1
Acris crepitans	4	*Pseudacris triseriata*	1

Table 7. *Estimated biomass (grams per hectare) of main prey species taken annually by 12 species of snakes, Natural History Reservation, Lawrence, Kansas.*

Prey species	*Agkistrodon contortrix*	*Carphophis vermis*	*Coluber constrictor*	*Crotalus horridus*	*Diadophis punctatus*	*Elaphe obsoleta*	*Lampropeltis calligaster*	*Lampropeltis triangulum*	*Nerodia sipedon*	*Pituophis melanoleucus*	*Storeria dekayi*	*Thamnophis sirtalis*
Earthworms												
Allolobophora caliginosa		435			11,878					—	210	12
Insects												
Acheta assimilis			84						—			—
Ceuthophilus maculatus			42									
Melanoplus spp.			137									—
Tettigoniidae			39									
Tibicen pruinosa	44											
Tipulidae					197							
Lepidoptera	12											
Amphibians												
Acris crepitans									4			
Bufo americanus									10			104
B. woodhousei					—	—	—	—	—	—	—	42
Gastrophryne olivacea	9											
Hyla chrysoscelis												73
Rana blairi	22		17			18	—	—	22	—	—	310
R. catesbeiana									100			83
Reptiles												
Carphophis vermis	7				—	—	—	4				
Coluber constrictor	11		135	3	—	—	1					
Diadophis punctatus	50		23	—	—	—	—	4				
Elaphe obsoleta	4		35									
Eumeces fasciatus	38		43	—	—	2	4	9				
E. obsoletus	2		42	—	—	—	2	3				
Ophisaurus attenuatus	46		13	—	106		3					
Thamnophis sirtalis	5		145		—	—	3					
Birds												
Cardinalis cardinalis			—			12						
Cyanocitta cristata						11						
Mammals												
Blarina brevicauda	92	—	40			3	1					
Cryptotis parva	38		12	—	—		4	2				
Microtus ochrogaster	640		1,010	38	—	111	57	—	—	45		62
Mus musculus	14			7		2	4			5		
Neotoma floridana	18		—	48	—	70	—		—	130		
Peromyscus leucopus	208		200	5		50						56
P. maniculatus			17				4			24		
Pitymys pinetorum	143			10		35	5			9		
Reithrodontomys megalotis	35		34									4
Scalopus aquaticus			75				37					
Sciurus carolinensis				78								
S. niger				104								
Sigmodon hispidus	52		86	6	—	—	4			15		
Sylvilagus floridanus	15		43	165		174	12			15		
Synaptomys cooperi	11						2					
Tamias striatus	19			1		1						

Relatively large prey samples were obtained from *Diadophis punctatus*, *Coluber constrictor*, *Agkistrodon contortrix*, *Elaphe obsoleta*, and *Thamnophis sirtalis*. No records were obtained for *Storeria dekayi*, but it is assumed to be an earthworm and mollusc eater (Wright and Wright 1957). Records for *Pituophis melanoleucus*, *Crotalus horridus*, *Lampropeltis triangulum*, and *Nerodia sipedon* were too few to show the full range of prey for those species.

As in other predators, snake food habits are controlled largely by prey availability (see Reynolds and Scott, this volume). Each of the 12 kinds of snakes studied depended to a large extent on one kind of prey, and in each instance it was one of the most abundant species in the local community. Four species of snakes, *Agkistrodon contortrix*, *Coluber constrictor*, *Elaphe obsoleta*, and *Lampropeltis calligaster*, had *Microtus ochrogaster* as their chief prey, and in three species (*Diadophis punctatus*, *Carphophis vermis*, and presumably *Storeria dekayi*) earthworms (mostly *Allolobophora caliginosa*) were the favorite. Other commonly taken prey were *Sylvilagus floridanus* for *Crotalus horridus*, *Neotoma floridana* for *Pituophis melanoleucus*, *Rana catesbeiana* for *Nerodia sipedon*, *Rana blairi* for *Thamnophis sirtalis*, and *Eumeces fasciatus* for *Lampropeltis triangulum*. Although insects seemed to offer the most available food sources within the size range of prey eaten by most of the snake species, they were scarcely used. Only three species ate them at all, and these took only certain types which made up a relatively small proportion of their total food volume.

Food habits of all 12 species discussed are well documented in the literature, and for each the trend shown by published records is somewhat different from that found on the Reservation. In some instances availability may be involved, but in others there may be innate preferences that differ in local populations. An outstanding example is *Diadophis punctatus*, a transcontinental species differing strikingly in size, appearance, habits, and habitats in different parts of its range. In the Great Lakes region, small terrestrial salamanders make up most of its food, whereas in the southeastern States it has been recorded as feeding on a wide variety of insects and other invertebrates. In the Southwest, where it is remarkably large, it is mainly a snake eater, but on the Reservation it takes earthworms almost exclusively (Fitch 1975).

Biomass of Food

Any attempt to quantify the feeding of snakes must take into account the different sizes of prey species. Each kind of snake tends to take prey within a certain size range, the largest individuals take the largest prey (see Reynolds and Scott, this volume). A wide range of size exists between and within species in the local populations (Table 1). The two largest species average more than 100 times the weights of the two smallest, and in some of the species the largest individuals weigh more than 100 times as much as the smallest ones.

The intact prey removed from the stomachs of live snakes was weighed when feasible, and these weights were used in calculating amounts of food consumed (Tables 5 and 6). However, in many instances prey identified from scats or from partly digested stomach items were not suitable for weighing. In lieu of individual weight, the weight considered most typical of the particular prey species was arbitrarily assigned for each such occurrence. A few of the larger prey species, notably the cottontail, were usually taken as immatures by local snakes, and this was taken into account in calculating their biomass. The insects eaten were nearly all of the largest local kinds (lepidopteran larvae, cicadas, crickets, katydids, and grasshoppers), and *Acheta assimilis*, *Ceuthophilus maculatus*, *Tibicen pruinosa*, *Melanoplus bivittatus*, *M. femurrubrum*, *M. differentialis*, *Arphia simplex*, and *Neoconocephalus robustus* made up most of the insect material. For each insect occurrence a biomass of 1 g was arbitrarily assumed. A series of earthworms from *Diadophis* stomachs averaged about 0.5 g, and this figure was used as the biomass represented by each earthworm occurrence.

For vertebrate prey, the following weights (in grams) were arbitrarily assigned to calculate biomass: *Acris crepitans* 3, "bird" 20, bird egg 10, *Blarina brevicauda* 10, *Bufo americanus* 10, *Bufo woodhousei* 10, *Cardinalis cardinalis* 20, *Carphophis vermis* 6, *Cnemidophorus sexlineatus* 10, *Coluber constrictor* (juvenile) 20, *Cryptotis parva* 5, *Cyanocitta cristata* 50, *Diadophis punctatus* 4, *Elaphe obsoleta* (juvenile) 20, *Eumeces fasciatus* 6, *Eumeces ob-*

soletus 25, "frog" (ranid) 15, *Gastrophryne olivacea* 4, *Hyla chrysoscelis* 10, *Microtus ochrogaster* 30, *Mus musculus* 15, *Peromyscus maniculatus* 18, *Peromyscus leucopus* 18, *Ophisaurus attenuatus* 30, *Pitymys pinetorum* 30, *Pseudacris triseriata* 3, *Rana blairi* 10, *Rana catesbeiana* 20, *Reithrodontomys megalotis* 10, *Sayornis phoebe* 15, *Scalopus aquaticus* 90, *Scincella lateralis* 2, *Sigmodon hispidus* 50, "shrew" 8, "snake" 50, *Sylvilagus floridanus* (juvenile) 150, *Thamnophis sirtalis* (juvenile) 20, and *Zapus hudsonius* 15.

The amount of food consumed by an individual snake varies according to the snake's size, sex, appetite, availability of prey, weather, season, and many other factors. In *Diadophis punctatus* it was determined that a single meal averaged about 12% of the snake's weight. Intervals between feedings averaged about 8 days, of which the first 4 days are required for digestion, and the snake has an empty digestive tract for the last 4 days. At this rate of feeding the snake would take about 27 meals ingesting about three times its body weight in a normal growing season estimated at 213 days. In *Diadophis*, the relatively small size of the snake itself, and the unprotected naked body and high surface-to-volume ratio in the elongate earthworm prey all promote rapid digestion and relatively large intake of food by the snake.

In contrast, *Agkistrodon contortrix* took prey averaging 18.5% of body weight. The snake has about eight meals per growing season totalling no more than 200% of body weight. Low metabolism associated with sluggish behavior reduces the food requirement, and the relatively massive prey, usually with protective hairy or scaly skin, delays digestion.

Comparable quantitative data concerning food requirements are not available for the other species studied. However, it might be expected that the two other small earthworm eaters, *Carphophis vermis* and *Storeria dekayi*, would resemble *Diadophis punctatus* in their food consumption, estimated at three times body weight annually, and the same figure is accepted for the natricines, *Thamnophis sirtalis* and *Nerodia sipedon*.

Coluber constrictor tends to maintain through behavioral thermoregulation (Fitch 1956, 1963*a*) a body temperature markedly higher than any of the other species. It is active and feeds on relatively small prey animals, mak-

Table 6. *Samples of 12 species of snakes from the Natural History Reservation, Lawrence, Kansas, showing composition of their populations (exclusive of first-year young) with estimates of the biomass of each species, and the biomass of its annual food consumption.*

Species	Time of sample	Number of snakes in sample	Ratio of adults to immatures	Ratio of males to females	Estimated biomass (kg/ha)	Estimated annual food consumption (multiples of body weight)	Estimated annual food biomass (kg/ha)
Agkistrodon contortrix	1977	100	4.26	1.22	0.80	2.0	1.60
Carphophis vermis	1949–1961	100	2.85	1.27	0.15	3.0	0.45
Coluber constrictor	1960–1961	100	1.33	0.98	0.60	4.0	2.40
Crotalus horridus	1949–1963	45	1.50	1.60	0.16	2.5	0.40
Diadophis punctatus	1971–1973	1,398	1.21	1.76	5.06	3.0	15.18
Elaphe obsoleta	1949–1977	100	5.25	1.05	0.23	2.5	0.58
Lampropeltis calligaster	1949–1977	100	4.26	1.73	0.05	2.5	0.13
L. triangulum	1949–1976	88	2.67	1.39	0.01	2.5	0.02
Nerodia sipedon	1949–1976	80	3.50	0.60	0.05	3.0	0.15
Pituophis melanoleucus	1949–1977	100	2.57	1.20	0.08	2.5	0.20
Storeria dekayi	1950–1977	85	0.98	0.85	0.07	3.0	0.21
Thamnophis sirtalis	1964–1974	150		0.76	0.25	3.0	0.75

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ing new captures before earlier prey is digested, so that several items may accumulate in the stomach. Because of these habits *Coluber constrictor* is believed to take a relatively greater biomass of prey than any of the other local species, and an annual food consumption four times body weight is estimated (Table 6).

The remaining five species (*Elaphe obsoleta*, *Lampropeltis calligaster*, *Lampropeltis triangulum*, *Pituophis melanoleucus*, and *Crotalus horridus*) all take relatively large prey animals which usually have protective hairy, scaly, or feather-covered surfaces and are relatively resistant to digestion. The food requirements of these species are believed to be relatively less than in *Diadophis* but more than *Agkistrodon*, and are estimated at 2.5 times body weight per growing season in Table 6. In this table, the biomass of each snake species is estimated on the basis of population density and average adult weight; and from these figures average annual food consumption for each is estimated: 2 times body weight for *Agkistrodon*, 3 times body weight for the small worm-eating species and natricines, 4 times body weight for *Coluber*, and 2.5 times body weight for the remaining species.

Diadophis punctatus, because of its great abundance, takes more food than all the other species combined; most of the remaining biomass is taken by *Agkistrodon contortrix* and *Coluber constrictor* (Table 5). Also, the biomass of the earthworm prey exceeds that of all other prey animals combined; only a few other species (*Microtus ochrogaster*, *Sylvilagus floridanus*, *Peromyscus leucopus*, *Rana blairi*) made up significant percentages of the total biomass, and all were among the commonest local small vertebrates.

Estimates of overlap in kinds and amounts of food taken by 12 snake species are shown in Table 7. This table is based mainly on the figures for prey species shown in Table 4, but it also utilized many additional records of prey animals less specifically determined. For example, *Thamnophis sirtalis* and *Nerodia sipedon* overlapped in their feeding, both having eaten 10 g of *Bufo americanus*, 22 g of *Rana blairi*, and 83 g of *Rana catesbeiana* – altogether 115 g constituting 15% of the total prey for *Thamnophis* and 78% of the total food intake for *Nerodia*.

Most of the species' diets overlap many of the others. *Lampropeltis calligaster* and *Pituophis* each overlap strongly (≥50%) with four other species; no other snake's diet overlaps strongly with more than two others. The food biomass of *Diadophis*, being so large, is not impacted great-

Table 7. *Estimated percentage overlaps in kinds and amounts of food taken by 12 snake species. Natural History Reservation, Lawrence, Kansas. Tabled numbers are percentages of the diets of snakes in the left-hand column that are shared with the snakes listed across the top; for example, an amount equivalent to 65% of the diet of* Agkistrodon *was also taken by* Coluber, *and 6% was shared with* Crotalus. *See text for methods of calculation. T = trace, <1% shared.*

Species	*A. contortrix*	*C. vermis*	*C. constrictor*	*C. horridus*	*D. punctatus*	*E. obsoleta*	*L. calligaster*	*L. triangulum*	*N. sipedon*	*P. melanoleucus*	*S. dekayi*	*T. sirtalis*
Agkistrodon contortrix	–	0	65	6	0	16	6	1	1	7	0	9
Carphophis vermis	0	–	0	0	100	0	0	0	0	0	48	3
Coluber constrictor	44	0	–	4	1	9	5	1	1	4	0	5
Crotalus horridus	25	0	22	–	0	63	15	0	0	27	0	11
Diadophis punctatus	0	3	T	0	–	0	T	0	0	0	1	T
Elaphe obsoleta	44	0	39	44	0	–	13	T	3	18	0	23
Lampropeltis calligaster	69	0	94	46	2	57	–	4	0	53	0	43
L. triangulum	86	0	91	0	0	11	29	–	0	6	0	0
Nerodia sipedon	15	0	12	0	0	12	0	0	–	0	0	78
Pituophis melanoleucus	52	0	50	54	0	51	36	1	0	–	0	23
Storeria dekayi	0	100	0	0	100	0	0	0	0	0	–	6
Thamnophis sirtalis	19	2	18	6	2	17	8	0	15	6	2	–

ly by any other species; however, the *Diadophis* diet completely overlaps the diets of the other two small earthworm-eaters. In the two partly aquatic species, *Nerodia* and *Thamnophis*, diets overlap only weakly with those of most other species.

Intraspecific Partitioning of Food Resources

The wide size range between the largest adults and the smallest hatchlings (Table 1) make possible a wide choice in size and type of prey. At one extreme hatchlings of *Carphophis vermis* and *Diadophis punctatus* and neonates of *Agkistrodon contortrix* are relatively large compared with average adults (weight ratios of young to adult 18.0, 21.0, and 10.6%, respectively) whereas at the opposite extreme neonates of *Nerodia sipedon* and *Thamnophis sirtalis* are relatively much smaller (weight ratios of young to adults 2.4 and 2.7%, respectively) and consequently have greater potential for partitioning of food resources. In the more stenophagous species, notably the earthworm-eaters (*Carphophis vermis* and *Diadophis punctatus*), young and adults differed only in the size of prey taken, but in some other species, adults and young subsist on different sets of prey.

In *Agkistrodon contortrix*, there was almost no overlap in prey species taken by adults (mainly *Microtus ochrogaster*, *Peromyscus leucopus*, *Pitymys pinetorum*, and *Blarina brevicauda*) and by first-year young (*Cryptotis parva*, *Diadophis punctatus*, *Eumeces fasciatus*, and *Gastrophryne olivacea*). Intermediate-sized second-year young overlapped both first-year young and adults in their feeding, but took some types of prey (cicadas, small mice, sphingid, and other caterpillars) more often than either.

In *Thamnophis sirtalis*, partitioning was also clear cut. Seven instances of predation on earthworms were all by first-year young (snout-vent [S–V] 226 ± 15 mm), whereas seven instances of predation on mammals were all by adults (S–V 666 ± 16 mm). Ranid frogs (*R. blairi* and *R. catesbeiana*) made up more than half the estimated total of food biomass, but even the smallest were too large for small garter snakes; the snakes that ate ranid frogs (N = 24) averaged S–V 541 ± 23 mm. Those that ate toads (N = 14) averaged S–V 428 ± 32 mm, partly because the newly metamorphosed young of both *Bufo americanus* and *B. woodhousei* are small enough to be eaten by neonate garter snakes.

In *Coluber constrictor* the 49 prey species were almost evenly divided between vertebrates and invertebrates. Many of the former including *Sylvilagus*, *Sigmodon*, *Scalopus*, and *Microtus* were too large for any but large adult snakes. First-year snakes were poorly represented in the sample; their food (grasshoppers, crickets, cave crickets, young voles) were of the same species represented in much larger numbers in the food of adults.

The food samples of *Crotalus horridus*, *Elaphe obsoleta*, and *Pituophis melanoleucus* were too small to demonstrate whether the young of these species took kinds of prey not used by adults, but most of the adults' food biomass was obtained from species too bulky to be swallowed by young – *Sylvilagus floridanus*, *Sciurus carolinensis*, *S. niger*, *Sigmodon hispidus*, and *Neotoma floridana*.

In several of the 12 snake species, there is a pronounced size difference between the sexes; females were much larger than males in *Nerodia sipedon*, *Thamnophis sirtalis*, *Diadophis punctatus*, *Carphophis vermis*, and *Coluber constrictor*, but males were larger than females in *Agkistrodon contortrix* and *Crotalus horridus*. In a series of 38 adult *Agkistrodon* (S–V > 500 mm) containing food in 1977, 59% of the males but only 36% of the females had eaten *Microtus ochrogaster*. The remaining 64% of females had eaten smaller prey: mice of three species, lizards, ringneck snakes, shrews, and cicadas. In *Coluber constrictor*, the larger adult females took a higher proportion of vertebrate prey and the smaller adult males took more insects. In 72 instances of predation on vertebrates (mostly voles and white-footed mice) by *Coluber* (S–V > 600 mm), 30.5% were by males, but in 175 instances of predation on insects, 45% were by males. Day-to-day trailing of racers equipped with radio transmitters showed that the males spent far more time than females above ground climbing in low trees, in situations where foliage-living insects would be available (Fitch and Shirer 1971). *Thamnophis sirtalis* subsisted chiefly on amphibians, but in six instances large adult females had eaten voles (three *Microtus ochrogaster*) or large mice (three *Peromyscus leucopus*); the only instance of predation on mammals by an adult male was on the much smaller *Reithrodontomys megalotis*. In general it seems that small mammals constitute a food resource used by adult females, reducing their competition with both adult males and immatures.

Discussion and Summary

The foregoing account indicates that many species of snakes coexist in high population densities, sharing certain available resources to varying degrees. Each must affect all its ecological associates, but direct interactions are difficult to observe. Food is the most obvious limiting resource. Contests between individuals over possession of a specific food object have never been observed in nature, and must be extremely rare, although they can be elicited in snakes confined together under crowded conditions. Competition is almost always exploitative; with regard to food it consists of the eating of prey by one individual, thereby rendering it unavailable to another.

However, all the common prey animals, such as earthworms, voles, white-footed mice, frogs, and rabbits are usually present in quantities beyond the needs of the snake population and are used by various non-ophidian predators also. The prey populations are subject to much greater fluctuations than those occurring in the snakes, and at times at least, their populations seem to be controlled by density-independent climatic factors.

The generation time of the snake predator is relatively lengthy compared with that of its prey. If it attains a normal life-span, a snake lives through major changes in the level of its prey populations. The relatively long life-span and a remarkable capacity for fasting enables the snake to survive drastic changes in the status of its prey. Unlike some other types of predators the snake is neither starved out nor forced to migrate by a scarcity of the favorite prey; instead it responds by reduced reproduction and partial shift to alternate prey species. In fact, the snake population is one of the most stable components of the overall biotic community, and probably exerts a stabilizing influence on the community as a whole.

Resources other than food supply are even less liable to be objects of direct competition. Water and shelter (for temporary resting places and hibernation) are the most obvious requirements. Dew and rain usually provide drinking water; when present at all, it is available to the entire population, and drinking by one snake does not deprive others. During periods of inactivity, shelters are readily shared, even by snake species that may, at other times, interact as predator and prey. Occupancy of a shelter by one individual does not usually prevent simultaneous use by others of the same or different species; it is common to find two or more snakes of different species together. In some instances coincidental use of a well-situated shelter may be involved, but also there may be mutual attraction as an adaptation to achieve physiological homeostasis, especially in hibernacula.

Indirect competition may function in a subtle fashion involving relations with predators and pathogens. A snake-eating predator, supported locally by a high population of one species, might have more effect on a second less common species because that species is more easily caught, or has a lower reproductive potential. Similarly, two or more coexisting species might be hosts of the same pathogen, but have different susceptibilities. If the commoner species were the less susceptible, it could act as a reservoir to maintain and transmit a pathogen severely limiting the less common species.

Earthworms, small mammals, and frogs, in that order, were the chief food resources for snakes on the study area; some 64 prey species, 40 in significant numbers, were being taken by the 12 species of snakes. Earthworms, estimated to make up just over 70% of the food biomass for the total snake population, were eaten by 99% of the individual snakes present. The three smallest species are almost entirely earthworm-eaters and occur in population densities of from 2 to 10,000 times greater than those of the nine largest species. The three small earthworm-eating species are similar in size but differ somewhat in habitat preferences (overlapping widely) and differ greatly in degree of fossorial adaptation.

Insects made up less than 10% of the prey biomass. They included mainly large orthopterans (*Acheta*, *Ceuthophilus*, *Melanoplus*, and *Neoconocephalus*) eaten only by *Coluber constrictor*, tipulid larvae eaten only by *Diadophis punctatus*, and cicada nymphs and sphingid larvae eaten mostly by *Agkistrodon contortrix*. All species of small mammals occurring on the area were found in the diets of the snakes, in roughly their order of abundance: *Microtus ochrogaster* (eaten by six species), *Peromyscus leucopus* (eaten by seven species), *Sylvilagus floridanus* (eaten by three species), *Neotoma floridana* (eaten by four species), *Pitymys pinetorum* (eaten by five species), *Sigmodon hispidus* (eaten by four species), *Scalopus aquaticus* (eaten by two species), and *Blarina brevicauda* (eaten by three species). *Sylvilagus floridanus*, *Sciurus carolinensis*, and *S. niger* are too large to be eaten as adults, except by unusually large individuals of the three largest snake species—*Crotalus horridus*, *Elaphe obsoleta*, and *Pituophis melanoleucus*. *Neotoma floridana*, *Sigmodon hispidus*, *Synaptomys cooperi*, *Microtus ochrogaster*, and *Pitymys pinetorum*, are also sufficiently large that, as adults, they are generally unavailable as food to the smaller species of mammal-eating snakes (*Coluber constrictor*, *Lampropeltis triangulum*, *Thamnophis sirtalis*) and to juveniles of the larger mammal-eating species.

Of the 12 species of snakes studied in broad ecological categories based on differences and similarities in habitat, microhabitat, size, food, and numbers (Table 8), no two are the same in all categories. In 16 of 66 paired species comparisons, the compared species differed in all seven categories. The greatest similarities (five of seven categories the same) were between *Diadophis punctatus* and *Storeria dekayi*, and between *Lampropeltis calligaster* and *Pituophis melanoleucus*.

Every one of the 12 snake species in this community possesses one or more unique traits in life style, habitat, or feeding specialization that greatly reduces the potential for competition with all associated species. These unique features may be summarized as follows. *Agkistrodon contortrix*, taking relatively very large prey items, concentrates its predation on the two most abundant species of small rodents, but also takes alternatively many types of mammals, birds, reptiles, amphibians, and two types of large insects, hunting by ambush and use of venom. *Carphophis vermis* is the only species specialized for fossorial existence, and is the most stenophagous of all, taking, insofar as known, only earthworms. *Coluber constrictor*, a grassland species, is unique in its active, visual search and pursuit of prey, and in the remar

Table 8. *Major ecological groupings of snake species on the Natural History Reservation, Lawrence, Kansas.*

Species	Major habitat	Microhabitat	Time of activity[a]	Method of securing prey	Adult weight range (g)	Population density per hectare	Chief food sources
Agkistrodon contortrix	Forest	Terrestrial	CN	Ambush, venom	75–300	1–9	Vole, mouse
Carphophis vermis	Forest	Fossorial	CN	Search, swallow	3–10	10–90	Earthworm
Coluber constrictor	Grassland	Terrestrial	D	Search, swallow	75–300	1–9	Vole, mouse
Crotalus horridus	Forest	Terrestrial	CN	Ambush, venom	300–1,000	< 1	Rat, squirrel, rabbit
Diadophis punctatus	Edge	Surface litter	D	Search, swallow	3–10	> 1,000	Earthworm
Elaphe obsoleta	Forest	Arboreal	DN	Search, constrict	300–1,000	< 1	Rat, squirrel, rabbit
Lampropeltis calligaster	Grassland	Terrestrial	DN	Search, constrict	75–300	< 1	Vole, mouse
L. triangulum	Edge	Surface litter	DN	Search, constrict	10–75	< 1	Reptile
Nerodia sipedon	Riparian	Aquatic	DN	Search, swallow	75–300	< 1	Anuran
Pituophis melanoleucus	Grassland	Terrestrial	DN	Search, constrict	300–1,000	< 1	Rat, squirrel, rabbit
Storeria dekayi	Edge	Surface litter	DN	Search, swallow	3–10	10–90	Earthworm
Thamnophis sirtalis	Riparian	Aquatic	D	Search, swallow	75–300	1–9	Anuran

[a] D = diurnal; C = crepuscular; N = nocturnal.

ably wide range of prey animals, including insects. *Crotalus horridus* is the largest of the species, and takes relatively large mammalian prey, too large to be taken by most of the others. It is an ambush hunter in forest habitat, using potent venom to immobilize the prey. *Diadophis punctatus* is the smallest species and is concentrated in edge habitats but is so successful and abundant that it occurs extensively in forest and grassland. It subsists almost entirely on earthworms, the most available of all prey species. *Elaphe obsoleta* is one of only two species with arboreal tendencies, and the only one with an important bird component in the diet. *Lampropeltis calligaster* is the species most limited to prairie habitat, and secures its prey by search and constriction, feeding mainly on small mammals, birds, and eggs. *Lampropeltis triangulum* is in a size range by itself, between the small and the medium-sized species; it is the only local snake that subsists chiefly on reptile prey, mostly lizards. *Nerodia sipedon* is the only strongly aquatic species. *Pituophis melanoleucus* is by far the largest of the grassland species and is specialized for predation on the pocket gopher (although no records were obtained in the small sample from the Reservation, where gophers are rare). *Storeria dekayi* is the only species known to take snails and slugs, although again, no records were obtained from the Reservation. *Thamnophis sirtalis* is most characteristic of a wetland habitat and amphibian diet.

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Use of a Mammalian Resource by a Chihuahuan Snake Community

by

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Abstract

Food habits and habitat selection were investigated in a snake community in northeastern Chihuahua, Mexico, from 1975 to 1977. A total of 418 snakes (20 species) was collected along Highway 16 from Villa Aldama to El Pastor. Examination of snake capture sites for the plant species present, and a study of structural characteristics of the vegetation and topographic features, showed that snakes exhibited distinct habitat preferences. Rodent species present and their relative densities were assessed by 5,400 trap nights at 18 trap stations. Digestive tracts of 351 snakes of 16 species yielded 153 food items. Rodents made up 71.1% of the diets by frequency of occurrence; lagomorphs, birds, reptiles, amphibians, and arthropods accounted for the remainder. The most important snake predators on rodents were *Crotalus atrox*, *C. molossus*, *C. scutulatus*, *Elaphe subocularis*, and *Pituophis melanoleucus*. The coexistence of mammal-eating snakes in this community is chiefly due to spatial habitat differences of predators which coincide with habitat variations of prey species; different-sized snakes chose optimal-sized prey in terms of catchability, handling, and potential danger.

Factors enabling competing species to remain in sympatry are not often clear. Much attention has been focused on isolating mechanisms (Gause 1934; Hardin 1960; Mayr 1963; Dobzhansky 1970; Levin 1970; Whittaker and Woodwell 1972; Lewontin 1974; Pielou 1974; Vance 1978). These authors agree that ecological isolation is probably the most important factor to continued coexistence.

The organization of animal communities may be a function of the range and variation of resources that ultimately determine the number of predatory species and the niche space of each. Associations of sympatric species may effectively reduce competition by their differential use of the trophic, temporal, and spatial components of an area (Pianka 1974*a*).

It is essential to quantify resource use among community members to understand the way resources are partitioned in a community. The ability to quantify available resources in a community is exceedingly difficult and oftentimes impossible. Community investigators to date have analyzed resource use by selecting and comparing those resource axes believed to be most important for coexistence of community members. Pianka (1974*b*) studied lizard communities by quantifying the use of food resources, time of activity, and habitat selection. Resource allocation in sympatric subalpine rodents was studied by Vaughn (1974) through dietary overlap, microhabitat selection, and activity. Brown and Lieberman (1973) studied the food and habitat axes of sand dune rodents. Habitat and food overlap were analyzed by Orians and Horn (1969) in a four-species blackbird community. None of these studies quantified the food resources available. Without this information, dietary overlap explains little of the dynamics of community structure (Conley 1976; Wiens 1977).

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Black (1974) studied a 17-species bat community in New Mexico and provided a detailed analysis of the insect resource available to it. He found that although the prey resources were highly diverse, only moths and beetles were very important to interactions within the bat community.

Arnold (1972) reviewed the food habits literature of sympatric snake species and provided strong empirical evidence that different species tend to eat different prey species. Shine (1977) listed other detailed studies of feeding habits in sympatric snakes that strengthen this conclusion. Arnold (1972) analyzed factors concerning species diversity gradients of predators and prey and provided four mechanisms which possibly cause sympatric snake species to eat different prey species: (1) habitat differences coinciding with habitat differences of prey species, (2) temporal differences in foraging activity coinciding with temporal differences in activity or availability of prey species, (3) differences of prey species eaten coinciding with different-sized prey species, and (4) innate differences in the tendency to strike different prey species. Arnold concluded that resource partitioning by snakes is accomplished by a variety of complex mechanisms. He believes that no single mechanism is solely responsible for relieving competition, but that all four act together to allow resource partitioning by snakes. Certainly, the importance of each mechanism will vary with any given community.

Specialized predators such as snakes are of similar basic morphology, but are different in size, foraging strategy, food capturing mechanisms, and prey eaten. Sympatry of closely related species of different sizes has been documented for a large number of animals (e.g., invertebrates – Wilson 1975; amphibians – Fraser 1976; reptiles – Schoener 1968; Pianka 1969; birds – Lack 1944; Ashmole 1968; mammals – Rosenzweig and Sterner 1970; Brown and Lieberman 1973). Size differences between the predator species and the manner in which the prey is hunted in addition to habitat segregation provide mechanisms whereby each predatory species can concentrate on a different set of prey species.

Although a number of studies have dealt with autecology of snakes (e.g., Fitch 1960, 1963, 1965; Hall 1969; Platt 1969; Clark 1970, 1974; Brown 1973; Branson and Baker 1974; Parker 1974; Clark and Fleet 1976), studies of the ecological relations of three or more snake species in the same community are few. Pough (1966) provided the first analysis of microhabitat partitioning among terrestrial snakes. The investigations by Fitch (1949) in California and those by Carpenter (1952) and Fleharty (1967) on *Thamnophis* represent the earliest such studies dealing with food resource partitioning of snakes. More recently, studies of food resource partitioning among three or more snake species include Barbault (1974), Mushinsky and Hebrard (1977), and Shine (1977). Although the above studies are important analyses of sympatric snake communities, they lack a quantitative assessment of the available prey resources.

The present study determines the use of a mammalian resource by a snake community in northeastern Chihuahua, Mexico. This is the first attempt to assess the prey resources available to a community of mammal-eating snakes. The purpose of this study was to determine to what extent coexistence of snakes in a community is related to partitioning of the food and habitat resources. Specific inquiries are posed as to the nature of food partitioning, the structure of the predator and prey communities, and the ways in which spatial and temporal niche dimensions of the individual prey and predators coincide.

Methods

Study Site

Field work was performed along an 80.5-km stretch of Mexico Highway 16, 22 km northeast of Chihuahua City from Villa Aldama to El Pastor. The area is at 29°10′ N and 105°30′ W at an elevation of 1,370 m. This region has hot summers and cold winters; maximum precipitation is in the summer and the average annual precipitation is 315 mm (Schmidt 1975).

The desert shrub formation of Chihuahua is uniform in physiognomy and simple in composition (Shreve 1939; Lesueur 1945). Topography consists of limestone mountains, gently falling bajadas, and broad intermont plains broken by numerous deep arroyos. The geology and soils are described by Morafka (1977). The vegetation is strongly dominated by creosote-bush (*Larrea tridentata*) in association with tarbush

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(*Flourensia cernua*) where the soil is thin, or with mesquite (*Prosopis glandulosa*) where the soil is deep. The otherwise monotonous uniformity is broken by ravines, dominated by catclaw mimosa (*Mimosa biuncifera*), Wright acacia (*Acacia wrightii*), and spiny hackberry (*Celtis pallida*). In the lowest part of each basin or valley, mesquite is dominant as a shrub 1 to 2 m tall. In surface depressions where water is likely to stand during some time of the year, there are no shrubs and the prevailing vegetation is an open sod of tobosa grass (*Hilaria mutica*). Important plants of the bajadas, in addition to creosote-bush and tarbush, include mariola (*Parthenium incanum*), ocotillo (*Fouquieria splendens*), and spiny allthorn (*Koeberlinia spinosa*). On the higher parts of the bajadas, on the pediments surrounding the mountains, and on the hills and mountain slopes, the vegetation is much more diverse. The most conspicuous plants are sotol (*Dasylirion scariosa*), ocotillo, rubber-plant (*Jatropha dioica*), lechuguilla agave (*Agave lecheguilla*), mariola, and soaptree yucca (*Yucca elata*).

Field Methods

Snakes were collected during automobile travel beginning at dusk (about 1930 h) over a period of 24 weeks between April and September 1975–77. In the course of three summers, 139 trips along Highway 16, totaling 16,713 km, provided records of 418 snakes. Additional snakes were hand-captured during the day and night while walking along the study route. Live snakes were retained in cloth bags which were examined for feces when the snake was removed. The following data were recorded for all snakes: exact location, time of capture, sex, size (snout-vent length [S–V], tail length, and head length [HL, the distance from the tip of snout to posterior end of mandible]). Measurements were recorded to the nearest millimeter on live and fresh-killed snakes with a meter stick and Peacock dial calipers. During 1975, all snakes captured alive (63) were permanently marked by clipping ventral caudal scales (Blanchard and Finster 1933) and released at the capture site. All dead snakes throughout the study, and snakes captured alive in 1976 and 1977, were preserved in 10% formalin and later transferred to a 55% isopropanol solution. They are deposited in the Museum of Southwestern Biology, University of New Mexico, Albuquerque.

Food Habits

In 1975 records of prey items were gathered through dissection of dead snakes (111) and by palping stomachs of living animals (41). All snakes (199) found during 1976 and 1977 were kept for dissection. The stomach and intestines of each snake were removed and examined for the presence of prey material. Condition of food items ranged from entire animals to body fragments or wads of hair retained in the lower tract. Animal fragments and hair were permanently mounted on microscope slides by techniques similar to those of Williamson (1951), Mayer (1952), and Brunner and Coman (1974). Additional slides (32) were prepared from fecal samples obtained from live snakes. Hair collected from the rodent and lagomorph species in the study area was used for reference slides for identification. Slides were examined under a dissecting microscope.

The features of hair useful for identification (medulla, cortex, cuticle) are not damaged during the digestive process (Brunner and Coman 1974). It was possible to identify hair slides to species in most instances. The only exception involved the two similar species, *Perognathus intermedius* and *P. penicillatus*, whose hair was indistinguishable. The habitat preferences of these rodents, however, are different (Anderson 1972; Findley et al. 1975). The rock pocket mouse, *P. intermedius*, was completely saxicolous, whereas *P. penicillatus* occurred in the lowest portions of the intermontane basins, often in association with mesquite. We determined which *Perognathus* species was represented on a particular hair slide on the basis of habitat (each record was considered to be a single prey item unless there were obviously more). Twelve snakes contained more than one prey item.

Rodent Size

The greatest width of a rodent skull (posterior zygomatic or bullae breadth) was used as a measure of prey size. Average measurements were obtained from Anderson (1972). This measure is used to determine the minimum size of a snake's gape necessary to ingest a particular rodent species.

Rodent Densities

Rodent species present and their relative densities were assessed by 5,400 trap nights at 18 trapping sites along the study route. Sites were selected to sample the five major habitat types common to the area. Three habitat types were sampled four times and two were sampled three times. At each site a square grid of 100 trap stations in 10 rows and columns was maintained for three nights for a total of 300 trap nights. Folding Sherman live traps placed at intervals of 10 paces were used. Voucher specimens were preserved in 10% formalin and later transferred to a 70% ethanol solution. They are deposited in the Museum of Southwestern Biology, University of New Mexico, Albuquerque. Several factors affect trapping results in various ways (Wiener and Smith 1972). The trapping results of this study are undoubtedly biased and are not appropriate for rigorous statistical analysis, but are valuable for showing trends.

Vegetation Classifications

Five vegetation types were determined within the study area on the basis of dominant species associations. These divisions agree with the major habitat types described by Shreve (1939). They are, in order of increasing plant diversity, slope, and rocky cover, (1) tobosa, (2) mesquite-grassland, (3) creosote-tarbush, (4), bajada, and (5) mountain pediment. The total number of road kilometers passing through each vegetation type was recorded and used to calculate the number of snakes per kilometer found in each.

Habitat Structure

Habitat structure was assessed at each snake capture site by establishing a 50- × 50-m square plot adjacent to the road in vegetation undisturbed by road construction. Conspicuous topographic features were noted (hills, rocks, alluvial fans). Plants more than 1 m tall were counted by walking in parallel lines through the plot, and those of questionable height were measured with a meter stick. Perennial species were recorded. This analysis was simple and provided a quick quantitative measure for recording vegetational physiognomy at each snake capture site.

Arena Studies

Feeding experiments were conducted in Chihuahua during the study to determine prey acceptance of snakes. These tests provided information on the variables of snake size, snake species, rodent size, and rodent species in relation to prey acceptance by snakes. A total of 64 snakes (12 species) and 11 rodent species was used in this testing. Individual snakes were placed singly into gravel-bottomed plywood and glass behavior boxes (100 × 100 × 50 cm) in a darkened room at 24–26°C, 24 h before the introduction of a single rodent. Rodents used were livetrapped in the study area. The rodent remained in the behavior box until it was killed and eaten or until 1 h elapsed, at which time both snake and rodent were removed. Generally an individual snake was used in only one test, but on a few occasions a snake was presented with a second rodent regardless of its reaction to the first. Individual rodents were not reused because by the end of one test they tended to become wary of snakes. Testing began at dusk (about 1930 h); a low-powered light source (shaded Coleman lantern) was used for observation.

Results

Mammal Community

Abundance and Habitat Preferences

In 5,400 trap nights, 243 individual mammals (13 species and three families of rodents) were captured at the 18 sites (Table 1). The most abundant species in the traps were *Dipodomys merriami*, *Peromyscus maniculatus*, *P. eremicus*, *Perognathus intermedius*, and *P. penicillatus* and accounted for 88.5% of all rodents captured. In addition to rodents, Audubon's cottontail (*Sylvilagus audubonii*) and the black-tailed jackrabbit (*Lepus californicus*) commonly were observed in the area, but their densities were difficult to judge. The distribu-

Table 1. *Total captures of rodents in study area, proportion of total catch, and proportion in snakes containing food, Chihuahua, Mexico, 1975-77. Trap data represent 5,400 trap nights at 18 stations.*

Species	Total captures	Percent of total	Percent in snakes with food
Dipodomys merriami	126	51.9	24.2
Peromyscus maniculatus	45	18.5	16.4
Perognathus intermedius	17	6.9	7.0
P. penicillatus	15	6.2	7.8
Peromyscus eremicus	12	4.9	5.5
Onychomys torridus	7	2.9	
Perognathus flavus	6	2.5	13.3
Spermophilus spilosoma	4	1.6	6.3
Sigmodon hispidus	4	1.6	3.1
Reithrodontomys megalotis	3	1.2	
Neotoma albigula	2	0.8	3.1
Spermophilus variegatus	1	0.4	0.07
Dipodomys spectabilis	1	0.4	7.8

tion of mammal species in the five habitat types (Table 2) shows that *Dipodomys merriami* and *Peromyscus maniculatus* were the most abundant species and, along with *Perognathus flavus*, they occurred in four of the five habitat types. Tobosa was the only habitat supporting large numbers of *Dipodomys spectabilis* and *Spermophilus spilosoma*. These species were underrepresented in the trapping accounts, but the high density of their mounds in tobosa indicates they were common. The greatest number of species was found in mesquite-grassland, but *Dipodomys merriami*, *Perognathus penicillatus*, and *Peromyscus maniculatus* were the only common species. *Onychomys torridus* and *Sigmodon hispidus* were found only in this habitat. In the bajada and mountain pediment, *Perognathus intermedius*, *Peromyscus eremicus*, and *Spermophilus variegatus* were common.

Rodents were most noticeable during the wet months, July to September. Although extensive trapping was not conducted before the wet season, rodents were seen more frequently on the road at night with the onset of summer rains.

Predatory Community

A total of 418 individuals representing 20 species of snakes in two families was found during the three activity seasons (Table 3). Of the 11 species containing mammal remains, 5 snake predators (*Crotalus scutulatus*, *C. atrox*, *C. molossus*, *Pituophis melanoleucus*, and *Elaphe subocularis*) accounted for 92.2% of the total predation by snakes on mammals. More than half the records of snake encounters (61.3%) were accounted for by the above five species; *C. atrox* and *C. scutulatus* alone represented 43.8%.

Of the five important mammal-eating snakes, males always averaged larger than females (Table 4). This has been previously reported for species of *Crotalus* by Klauber (1972). A comparison of the mean snout-vent length of the three *Crotalus* species reveals that *C. molossus* was the largest and *C. scutulatus* the smallest. Although it is common for *C. molossus* to be larger than *C. scutulatus*, it is unusual for it to be larger than *C. atrox*. Klauber (1972) showed that a "large adult male" of *C. atrox* was 500 mm larger than *C. molossus* and 600 mm larger than *C. scutulatus*. The largest adult males we recorded for *C. molossus* and *C. scutulatus* correspond closely to Klauber's data, but the largest *C. atrox* was 600 mm smaller than his record. The *C. atrox* from our study area were considerably smaller than those of many other areas. The two colubrids, *P. melanoleucus* and *E. subocularis*, are similar in length, but for any given size *P. melanoleucus* are heavier.

Distinct habitat preferences were found for these species in the Chihuahuan Desert shrub (Table 5). *Crotalus atrox* preferred the densest

Table 2. *Ranking of rodent species trapped in five habitat types along Highway 16 from Villa Aldama to El Pastor, Chihuahua, Mexico, 1975–77. Species are ranked in descending order from most abundant. Mesquite-grassland and creosote-tarbush were sampled three times; all others were sampled four times. See text for description of habitats and sampling method used.*

Habitat and Species	Number trapped
Tobosa	
Dipodomys merriami	18
Peromyscus maniculatus	15
Spermophilus spilosoma	4
Onychomys torridus	4
Perognathus flavus	2
D. spectabilis	1
Mesquite-Grassland	
D. merriami	37
Perognathus penicillatus	10
Peromyscus maniculatus	10
Sigmodon hispidus	4
Onychomys torridus	3
Reithrodontomys megalotis	2
Perognathus flavus	1
Neotoma albigula	1
Creosote-Tarbush	
D. merriami	41
Peromyscus maniculatus	16
Perognathus penicillatus	5
P. flavus	2
Reithrodontomys megalotis	1
Neotoma albigula	1
Bajada	
D. merriami	30
Perognathus intermedius	7
Peromyscus eremicus	4
P. maniculatus	4
Perognathus flavus	1
Mountain pediment	
Peromyscus intermedius	10
P. eremicus	8
Spermophilus variegatus	1

cover, whereas *C. scutulatus* preferred sparse shrub cover. Comparisons of shrub cover densities made between species showed a significant difference (Mann-Whitney "U," $P < 0.01$) between *C. atrox* and the other species but all other comparisons were nonsignificant. By comparing relative road abundances, preferences for certain habitats were evident (Table 6, Fig. 1). *Crotalus molossus* and *E. subocularis* were found almost exclusively in rocky areas; they were most common in the mountain pediment and bajada. The remaining three species were more broadly distributed. *Crotalus scutulatus* was the most common species in tobosa and was also common with *C. atrox* in the creosote-tarbush and bajada assemblages. *Crotalus atrox* rarely was found in tobosa. The most common species in mesquite-grassland was *P. melanoleucus*. A relation between vegetative density and lizard species densities has previously been documented in the Chihuahuan Desert of Big Bend, Texas (Degenhardt 1966, 1977).

None of the 63 snakes marked in 1975 were recaptured. Pough (1966) also obtained no recaptures of the 16 snakes he marked in southern Arizona.

Food Habits

Of 351 snakes examined, 153 (43.6%) contained food material. In addition, 32 fecal samples provided 22 identifiable items. Rodents made up 71.1% of the diets (by frequency of occurrence) and birds, reptiles, amphibians, and arthropods accounted for the remainder. There is a significant positive correlation ($r_s = 0.64$, $P < 0.05$) between rodent species abundance in traps and their frequency of occurrence in the diets of all snakes (Fig. 2).

There were important differences in the types of prey taken by different snake species that corresponded well with the habitat preferences of both predator and prey. The percentage frequency of occurrence of prey items in diets of the five mammal-eating snakes (Table 7) shows a greater number of prey species in the diets of the *Crotalus* than in the colubrids. The two most common rodents in the present study, *Dipodomys merriami* and *Peromyscus maniculatus*, were also the most common prey items. These two species, along with *Perognathus flavus*, accounted for 54.7% of the rodents found in snake stomachs.

The diet of *C. scutulatus* contained those rodents which were most abundant in tobosa. *Dipodomys merriami* was the commonest rodent in tobosa and was the most common mammal in the diet of *C. scutulatus* (Fig. 3). Likewise, tobosa supported the largest number of *Dipodomys spectabilis* and *Spermophilus*

Table 3. *Number and percentage of all snakes found on Highway 16 from Villa Aldama to El Pastor. Chihuahua, Mexico. 1975–77. Snake species containing mammal remains are noted by an asterisk.*

Species	1975		1976		1977		Total	
	No.	%	No.	%	No.	%	No.	
*Crotalus atrox**	41	20.5	24	17.3	14	17.7	79	18.9
*C. scutulatus**	50	25.0	35	25.2	19	24.0	104	24.9
*C. molossus**	9	4.5	6	4.3	5	6.3	20	4.8
*C. lepidus**	1	0.5	1	0.7	1	1.3	3	0.7
*Elaphe subocularis**	8	4.0	11	7.9	2	2.5	21	5.0
*E. guttata**	5	2.5	2	1.4	0	–	7	1.7
*Pituophis melanoleucus**	9	4.5	13	9.4	10	12.7	32	7.7
*Rhinocheilus lecontei**	14	7.0	9	6.5	6	7.5	29	6.8
*Arizona elegans**	14	7.0	5	3.6	7	8.9	26	6.2
*Lampropeltis getulus**	9	4.5	6	4.3	2	2.5	17	4.1
Heterodon nasicus	4	2.0	0	–	0	–	4	1.0
Thamnophis marcianus	16	8.0	12	8.6	2	2.5	30	7.2
T. cyrtopsis	3	1.5	0	–	1	1.3	4	1.0
Hypsiglena torquata	8	4.0	2	1.4	1	1.3	11	2.6
Masticophis flagellum	5	2.5	5	3.6	5	6.3	15	3.6
*M. taeniatus**	0	–	5	3.6	0	–	5	1.2
Trimorphodon biscutatus	2	1.0	0	–	1	1.3	3	0.7
Tantilla nigriceps	1	0.5	1	0.7	1	1.3	3	0.7
Salvadora deserticola	0	–	2	1.4	1	1.3	3	0.7
Sonora semiannulata	1	0.5	0	–	1	1.3	2	0.5
Total	200		139		79		418	

spilosoma, both of which had their highest frequency of occurrence in the diet of *C. scutulatus*. There is no significant positive correlation ($r_s = 0.64$, $P > 0.05$) between total rodent abundance and the frequency of occurrence of each species in the diet of *C. scutulatus*.

The most important rodents in the diets of *C. molossus* and *E. subocularis* were *Perognathus intermedius* and *Peromyscus eremicus* (Figs. 4 and 5). Although *C. molossus* was found most often in the mountain pediment, where *D. merriami* is absent, this rodent constituted as large a part of the diet of *C. molossus* as *P. eremicus*, a species found only in the rocky foothills and at higher elevations. *Crotalus molossus* seems to forage in those habitats containing

Table 4. *Comparison of sizes of five species of snakes from Chihuahua, Mexico, along Highway 16 from Villa Aldama to El Pastor, 1975–77.*

Species	Sex	Sample size	Mean snout-vent length ± standard error (mm)	Mean jaw length ± standard error (mm)
Crotalus atrox	Male	30	757.41 ± 2.4	36.82 ± 0.10
	Female	7	653.1 ± 5.1	34.64 ± 1.0
C. scutulatus	Male	33	671.11 ± 2.3	32.43 ± 0.45
	Female	14	601.9 ± 3.7	28.64 ± 0.43
C. molossus	Male	20	780.0 ± 9.9	40.65 ± 0.65
Pituophis melanoleucus	Male	7	917.43 ± 6.7	31.46 ± 1.0
	Female	10	865.24 ± 4.7	31.45 ± 0.85
Elaphe subocularis	Male	5	904.8 ± 5.4	32.0 ± 0.67
	Female	8	894.5 ± 5.2	31.68 ± 0.67

Table 5. *Comparison of density of plants over 1 m tall in 50- × 50-m plots for five species of snakes in Chihuahua, Mexico, 1975–77.*

Species	Number of plots	Mean number of plants ± standard error
Crotalus atrox	57	41.1 ± 0.7
Pituophis melanoleucus	22	33.8 ± 1.0
Elaphe subocularis	17	29.4 ± 0.9
C. molossus	20	27.3 ± 0.7
C. scutulatus	74	26.8 ± 0.5

D. merriami more often than the data in Table 6 indicate. No significant correlation exists between rodent species abundance and their frequency of occurrence in the diets of either *C. molossus* (r_s = 0.68, $P > 0.05$) or *E. subocularis* (r_s = 0.55, $P > 0.05$).

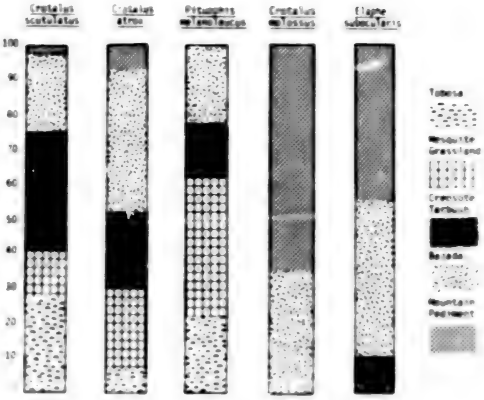

Fig. 1. Relative abundance of five mammal-eating snakes in various habitats during April-September 1975–77 from Villa Aldama to El Pastor, Chihuahua, Mexico.

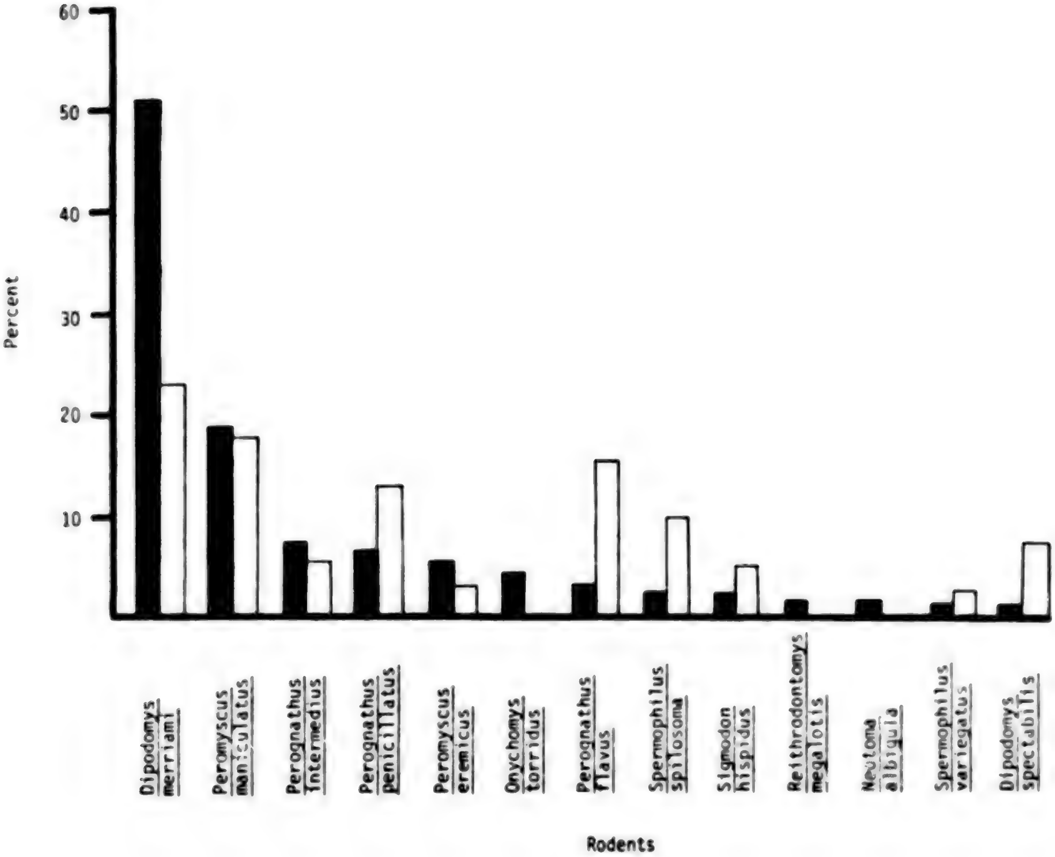

Fig. 2. Proportion of rodents trapped in study area (closed bars) and their frequency of occurrence in snakes containing mammals (open bars).

Table 6. *Relative abundance (no./km) and total number (in parentheses) of snakes collected in five habitats along Highway 16, Chihuahua, Mexico, 1975–77.*

Species	Habitat Tobosa	 Mesquite-grassland	 Creosote-tarbush	 Bajada	 Mountain pediment
Crotalus scutulatus	1.96	0.99	1.46	1.36	0.21
n = 104	(30)	(11)	(36)	(25)	(2)
C. atrox	0.33	1.62	0.89	1.58	0.52
n = 79	(5)	(18)	(22)	(29)	(5)
Pituophis melanoleucus	0.45	1.17	0.20	0.38	
n = 32	(7)	(13)	(5)	(7)	
C. molossus	–	–	–	0.38	1.34
n = 20	–	–	–	(7)	(13)
Elaphe subocularis	–	–	0.08	0.53	0.92
n = 21	–	–	(2)	(10)	(9)
Total km of each habitat	15.6	11.3	25.1	18.7	9.8
Percent of total habitat	19.37	14.03	31.18	23.22	12.17

Crotalus atrox and *P. melanoleucus* were most abundant in mesquite-grassland. The two most common rodents in the diets of each were *Dipodomys merriami* and *Peromyscus maniculatus* (Figs. 6 and 7). Both *Sigmodon hispidus* and *Perognathus penicillatus* were associated with mesquite-grassland and had the highest frequency of occurrence in the diet of *C. atrox*, but were absent in *P. melanoleucus*. A significant positive correlation (r_s = 0.66,

Table 7. *Percentage distribution by frequency of occurrence of prey species found in five species of snakes in the Chihuahua, Mexico, study area, 1975–77.*

Prey Species	Snake species *Crotalus atrox* (n = 43)	 *Crotalus scutulatus* (n = 48)	 *Crotalus molossus* (n = 12)	 *Pituophis melanoleucus* (n = 15)	 *Elaphe subocularis* (n = 12)
Sylvilagus auduboni	4.1	2.1	–	13.3	
Lepus californicus	–	4.2	–	13.3	
Spermophilus spilosoma	8.2	10.4	–	6.7	
S. variegatus	2.0	–	–	–	
Perognathus flavus	12.2	12.5	8.3	–	8.3
P. intermedius	4.1	2.1	25.0	–	16.7
P. penicillatus	10.2	6.2	–	6.7	
Dipodomys merriami	18.4	27.1	16.7	20.0	16.7
D. spectabilis	6.1	12.5	–	–	
Peromyscus eremicus	2.0	4.2	16.7	–	25.0
P. maniculatus	14.3	10.4	8.3	26.7	
Sigmodon hispidus	4.1	–	–	–	–
Neotoma albigula	–	–	8.3	–	16.7
Birds	2.0	–	16.7	13.3	16.7
Reptiles	12.2	–	–	–	–
Arthropods	–	8.3	–	–	

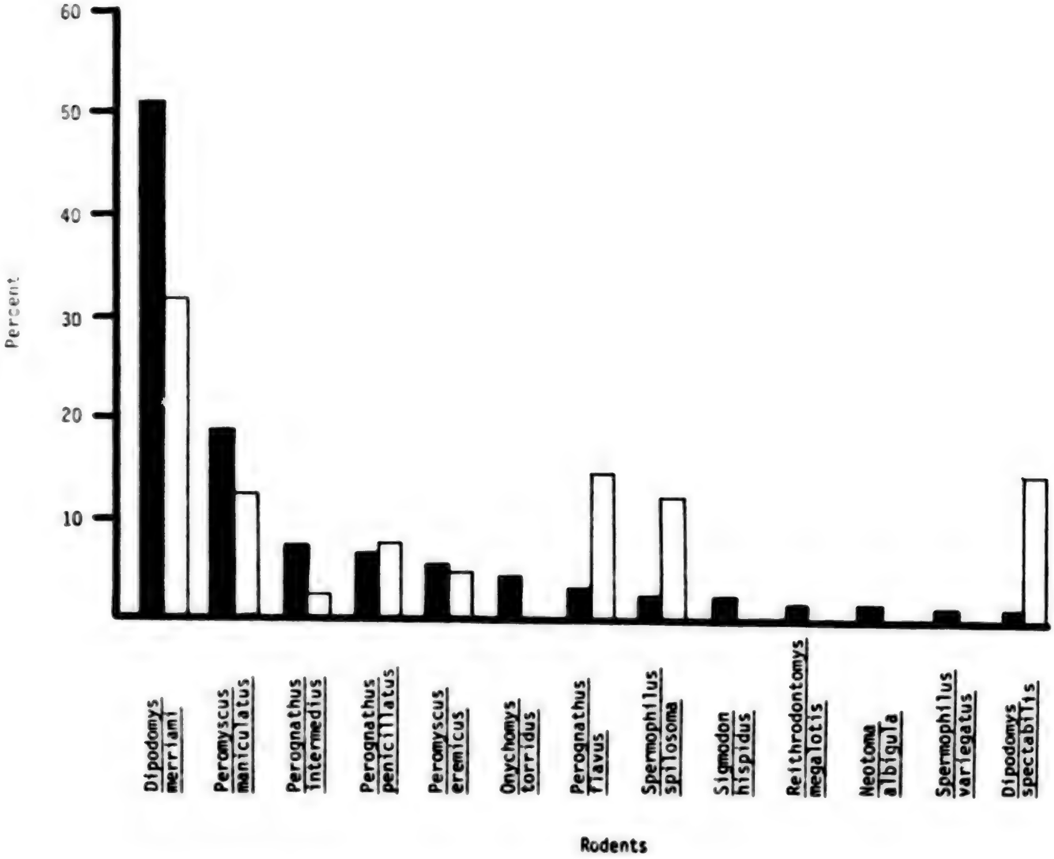

Fig. 3. Proportion of rodents trapped in the study area (closed bars) and the frequency of occurrence of each in the diet of *Crotalus scutulatus* (open bars).

$P < 0.05$) exists between the total abundance of rodents and their frequency of occurrence in the diet of *C. atrox*, but not for *P. melanoleucus* ($r_s = 0.55$, $P > 0.05$).

Present in the diets of *C. scutulatus*, *C. atrox*, and *P. melanoleucus* was *Sylvilagus auduboni*. The last two snakes also contained *Lepus californicus*. All rabbits and hares found in stomachs were immature; *Lepus californicus* was represented by nestlings.

The distributions of rodent size in individuals of *C. atrox* and *C. scutulatus* (Figs. 8 and 9) show significant ($P < 0.01$) positive correlations between snake head length and rodent skull size for each snake species, indicating that larger snakes ingested larger prey. When a snake attained a head length of 30 mm, it was able to ingest the two most common species, *Dipodomys merriami* and *Peromyscus maniculatus*. Below this head length *Perognathus flavus* was the most common rodent in the diets. Since food is swallowed whole, it is reasonable that large food items are handled more easily by larger snakes. This relation agrees with the findings of Fitch and Twining (1946) for *Crotalus viridis* and of Beavers (1976) for *C. atrox*.

Arena Studies

Cottam et al. (1959) stated that snakes often kill prey items that are much too large to ingest suggesting that there is no discretion of prey size made by a particular snake. On an energy expenditure basis, however, this does not seem reasonable.

In testing prey items, we found that snakes selected prey on the basis of size. As shown in Figs. 10 and 11, the smallest snakes rejected prey items too large for them to eat. Also, large

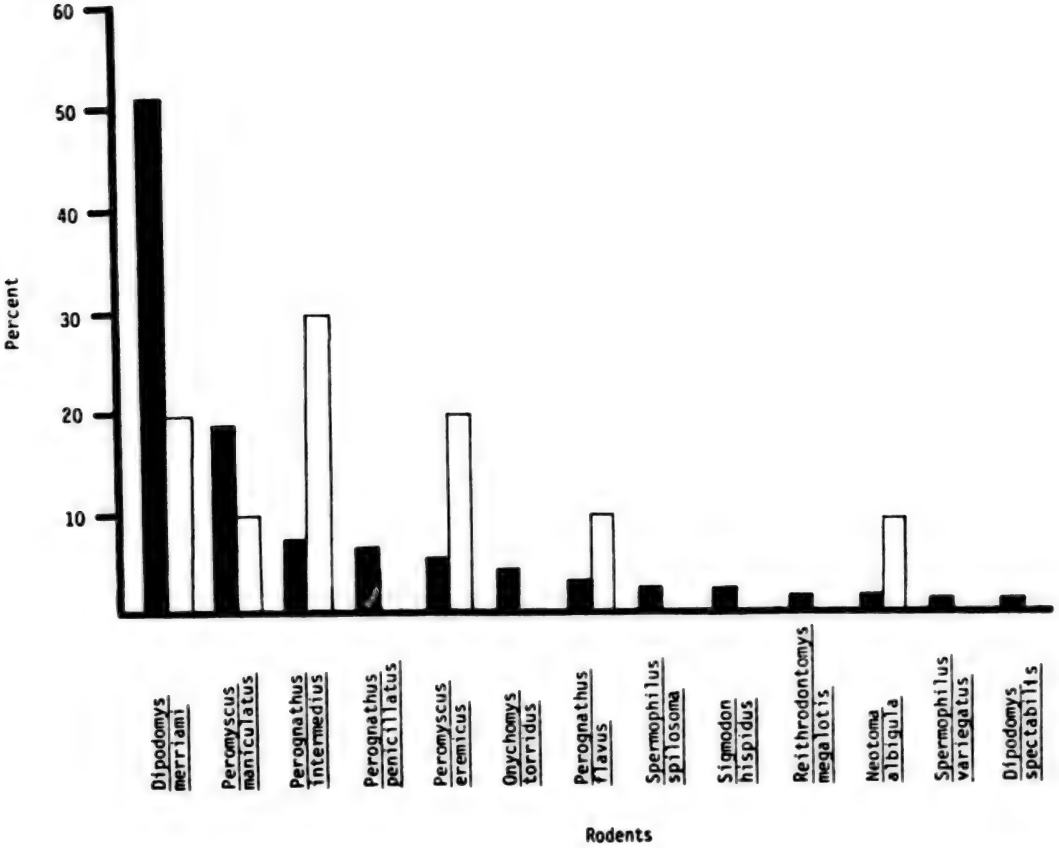

Fig. 4. Proportion of rodents trapped in the study area (closed bars) and the frequency of occurrence of each species in the diet of *Crotalus molossus* (open bars).

snakes tended to ignore the smallest prey items and concentrated on medium-sized rodents. Retreat from large rodents was exhibited by two *Crotalus scutulatus*. One snake (S–V 867 mm) moved continuously in order to maintain a maximum distance from a *Spermophilus variegatus* (the squirrel walked on the snake a number of times). The snake finally struck and disabled the squirrel, but afterwards continued to maintain a maximum distance from it. A second snake (S–V 787 mm) behaved similarly when a *Neotoma albigula* was offered. On this occasion, however, the rodent devoured a considerable amount of the snake's tail before the end of the test. During this time the snake continued to move about the arena and never attempted to strike the rodent.

The arena data show that snakes selected for catchability, handling, and potential danger of the optimal-sized prey item; they rejected individuals that were too small or too large and those that were potentially dangerous.

Discussion

Of the 20 snake species that occur in this community, 5 have sufficiently high populations to be important predators of rodents. The remaining species are limited in numbers and distribution on the study area, or do not eat mammals.

Interspecific competition may be lessened by partial ecological isolation. Habitat differences for these five snakes have been noted. Klauber's (1972) descriptions of the habitats favored by *Crotalus atrox* and *C. scutulatus* suggest that *C. scutulatus* generally is found in more barren areas than *C. atrox*. This was also true in the present study but a large degree of habitat

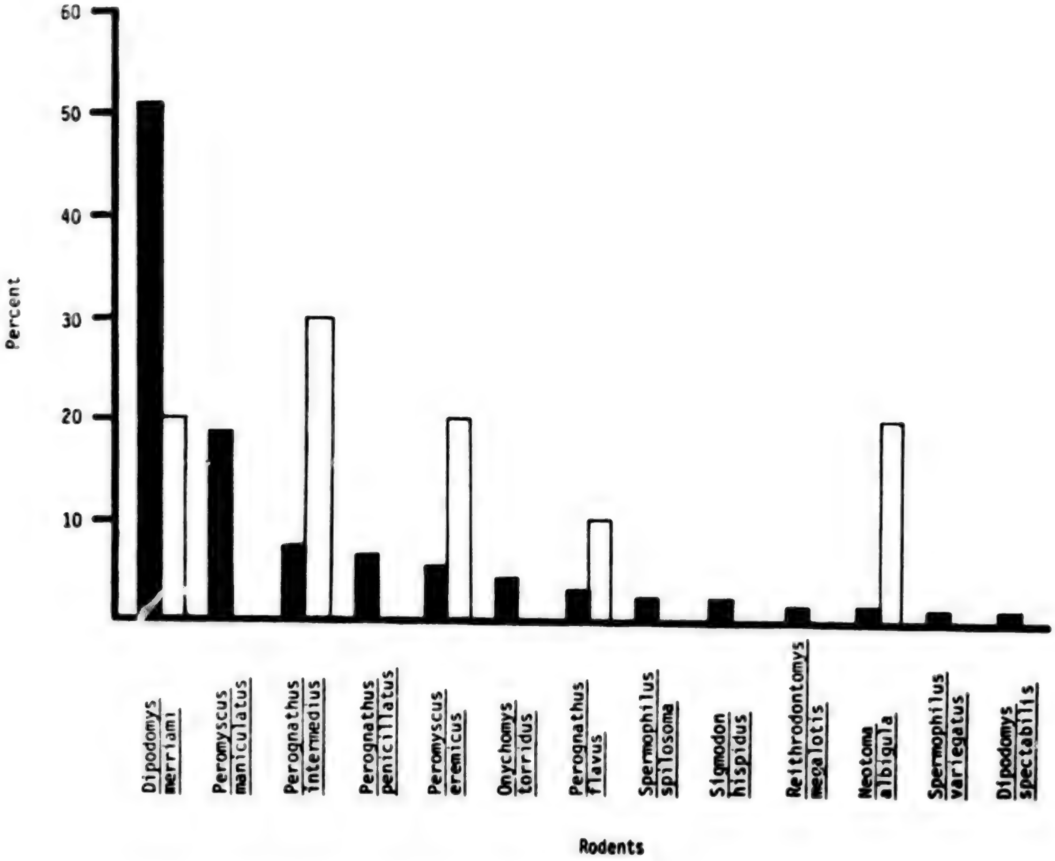

Fig. 5. Proportion of rodents trapped in the study area (closed bars) and the frequency of occurrence of each species in the diet of *Elaphe subocularis* (open bars).

overlap exists for these species and *Pituophis melanoleucus*. Pough (1966) also found considerable habitat overlap for these species in southeastern Arizona.

Although Klauber (1972) considered that sympatric populations of two or more species of rattlesnakes could be competitive, it is generally believed that this is only a temporary situation (Pough 1966 citing Mayr 1963). In this light, the broad overlap of *C. atrox* and *C. scutulatus* indicates that the species either are not competing or that the situation is unstable. Jacob (1977) described a situation in which *C. atrox* and *C. scutulatus* occur syntopically in an unstable desert grassland ecotone described by Morafka (1977) and postulated that these species may be able to coexist because their density is probably lower than in stable areas and the food supply may be exploited submaximally.

Although niche differences can be extremely subtle, apparently there is considerable similarity between the niches of *C. atrox* and *C. scutulatus*. It seems reasonable to assume, as did Klauber (1972), Damman (1961), and Pough (1966), that where they occur together these species are potential competitors. In view of their studies and the present study it appears that considerable habitat overlap is normal for these species, suggesting that their respective niches differ. Each species is most abundant in habitats and plant densities that are different from those of the other species.

In the study area *C. molossus* and *Elaphe subocularis* are almost entirely separated from *C. atrox*, *C. scutulatus*, and *P. melanoleucus*, and may experience reduced competition through differences in basic biology (size, morphology, venom vs. constriction) and foraging

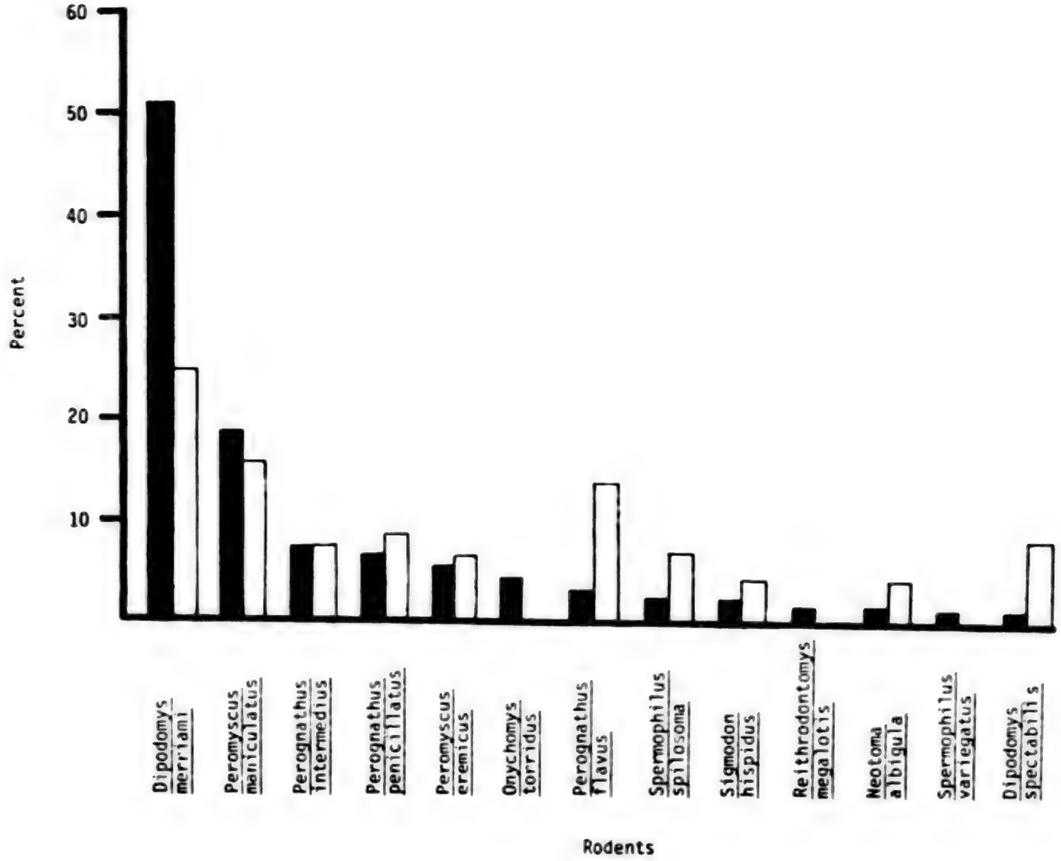

Fig. 6. Proportion of rodents trapped in the study area (closed bars) and the frequency of occurrence of each species in the diet of *Crotalus atrox* (open bars).

behavior (sit and wait vs. active foraging). Differences in biology would allow for reduced competition among *Pituophis melanoleucus*, *C. atrox*, and *C. scutulatus* where the three occur syntopically.

The prey community on which the snakes are actual or potential predators is diversified in terms of species, size, life forms, and behavior. Although a variety of rodents are used as prey, the data suggest that some are eaten more than others (e.g., *Dipodomys merriami*, *Peromyscus maniculatus*, *Perognathus flavus*). Considering that most adaptation is a compromise between [illegible] and abiotic selective factors, we cannot [illegible] a priori that prey is exploited at max[illegible] efficiency in a given predator-prey system. MacArthur and Levins (1964) provided a theoretical model in which an organism that limits the variety of resources it uses enhances its fitness. The use of certain prey would depress a predator's fitness if it has to expend more energy obtaining the food than it receives from it. Also, the potential hazard of certain prey items would reduce a predator's fitness. The predator would do better to invest the time and energy needed to obtain this prey item searching for a more rewarding one. It is probable that certain rodents, by virtue of their size, population density, ability to escape, activity patterns, fierceness, or habitat preferences, essentially might never be exposed to certain snake predators.

Perez et al. (1978*a*, 1978*b*) found that *Neotoma micropus*, *Spermophilus mexicanus*, and *Sigmodon hispidus* have naturally occurring antihemorrhagic factors in their blood which provide them with a high resistance to *Crotalus atrox* venom. It is probable that *N. albigula* and *S. variegatus* share such resistance. Cottam et al.

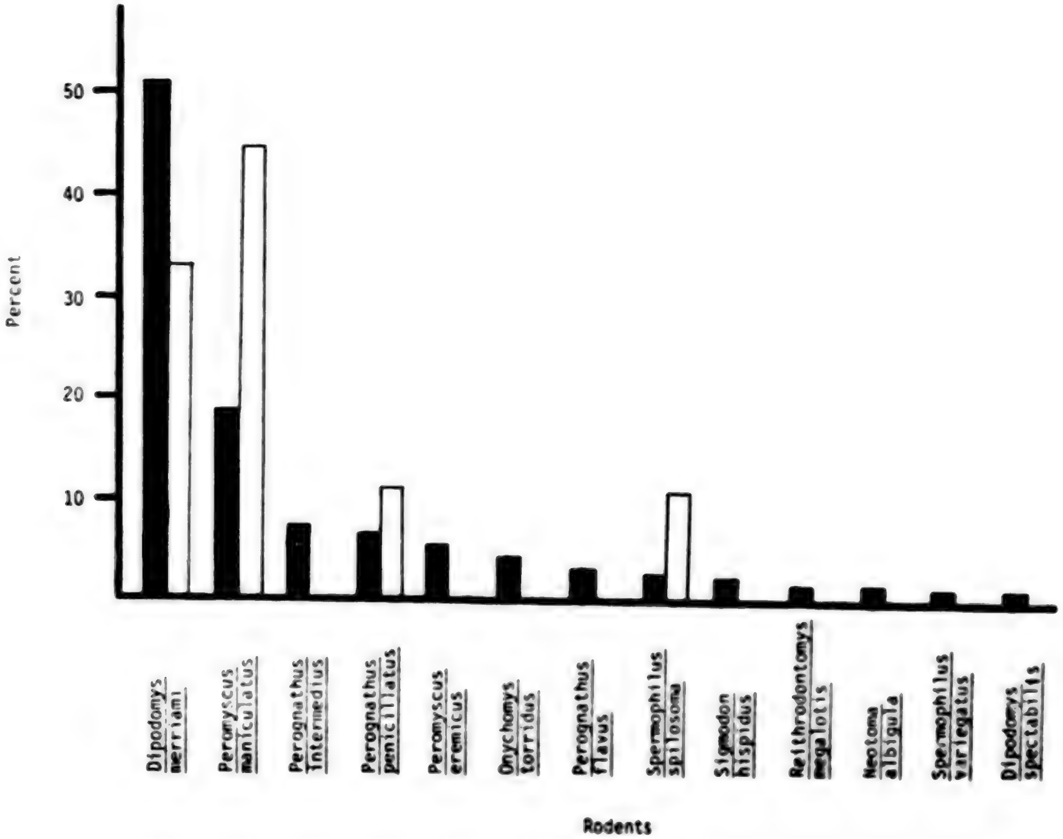

Fig. 7. Proportion of rodents trapped in the study area (closed bars) and the frequency of occurrence of each species in the diet of *Pituophis melanoleucus* (open bars).

(1959), on the Welder Wildlife Refuge in Texas, found that the two most important food items in the stomachs of *C. atrox* were *N. micropus* and *S. hispidus*. In the present study, *C. atrox* contained *S. hispidus* and *C. molossus* had *N. albigula* in their stomachs.

Natural resistance in these rodents is not surprising because they live in the same habitat as rattlesnakes and often in the same midden as woodrats. The carnivorous diet of rattlesnakes and their cohabitation with these rodents are two possible reasons for the evolved resistance of these animals to rattlesnake venom. It is apparent, however, that this defense against rattlesnake venom is not always effective. In terms of the evolution of the predator-prey system, the relation of snake venom toxicity and the degree of rodent resistance is a dynamic situation; the rodents are constantly evolving resistance, and snake venom is evolving to overcome this resistance. The cost of the system to the animals is unknown as is the mechanism of neutralization (Perez et al. 1978*b*).

Predator body size is an indicator of food size for some species of mammals (Rosenzweig 1966; McNab 1971; Brown and Lieberman 1973; Mares and Williams 1977), birds (see Schoener 1971 for references), lizards (Schoener 1968; Pianka 1969), and amphibians (Fraser 1976). Many snakes, as compared with other terrestrial endothermic vertebrates, do not sharply discontinue growth at sexual maturity. This results in more variation in adult size. The kind of prey taken depends on snake size; the smallest individuals are probably most restricted in terms of the kinds of prey used (Wilson 1975). Stomach content data (Table 7) show that lizards are included in the diet of young *Crotalus atrox* and

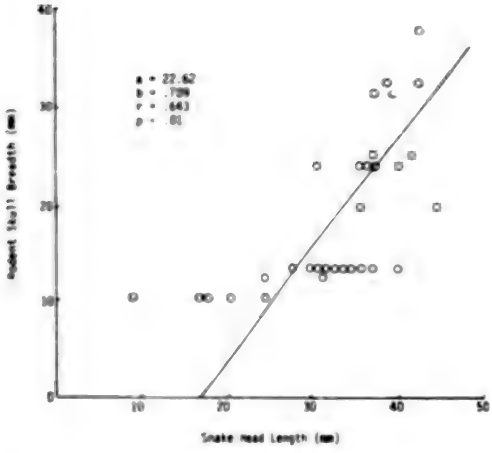

Fig. 8. Regression of head length of *Crotalus atrox* and average rodent prey skull breadth.

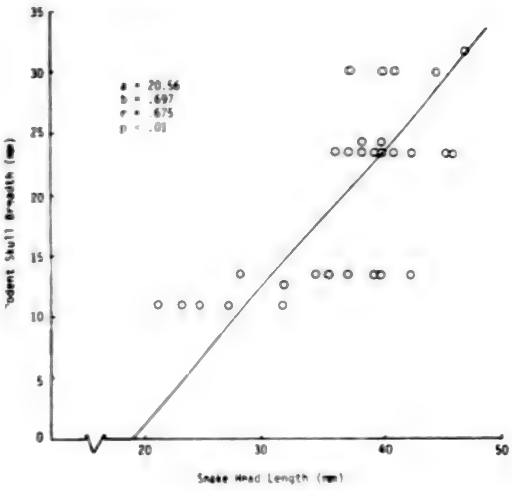

Fig. 9. Regression of head length of *Crotalus scutulatus* and average rodent prey skull breadth.

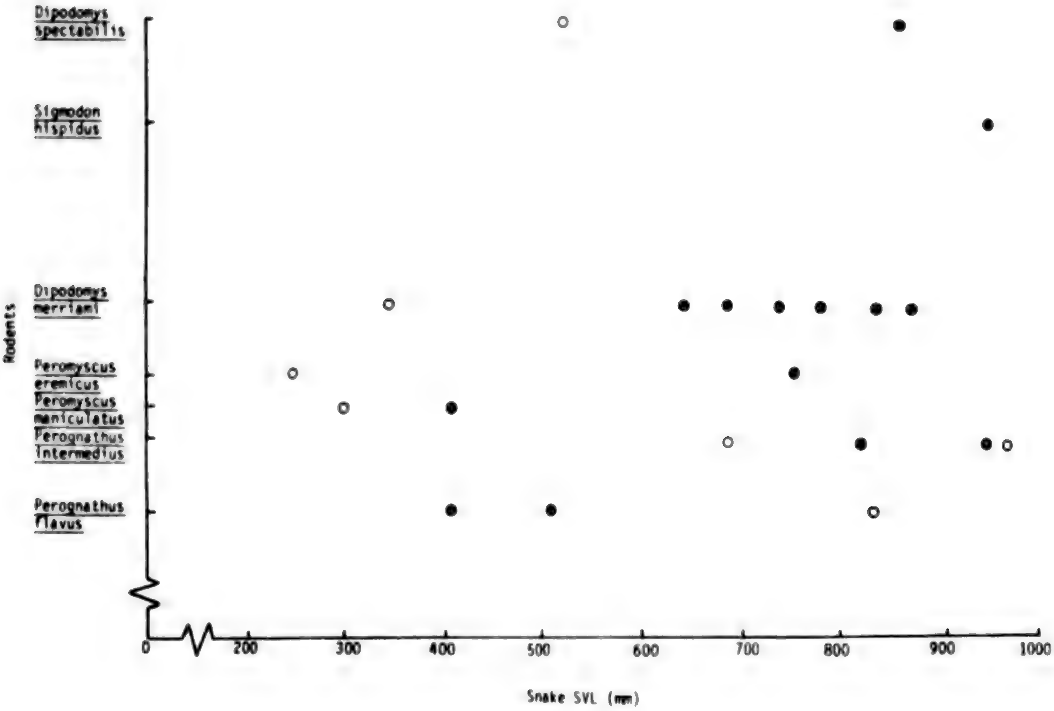

Fig. 10. Results of arena studies with *Crotalus atrox* showing acceptance (•) and rejection (○) of rodents introduced to various-sized snakes. Rodent position on ordinate proportional to average skull breadth, smallest at bottom.

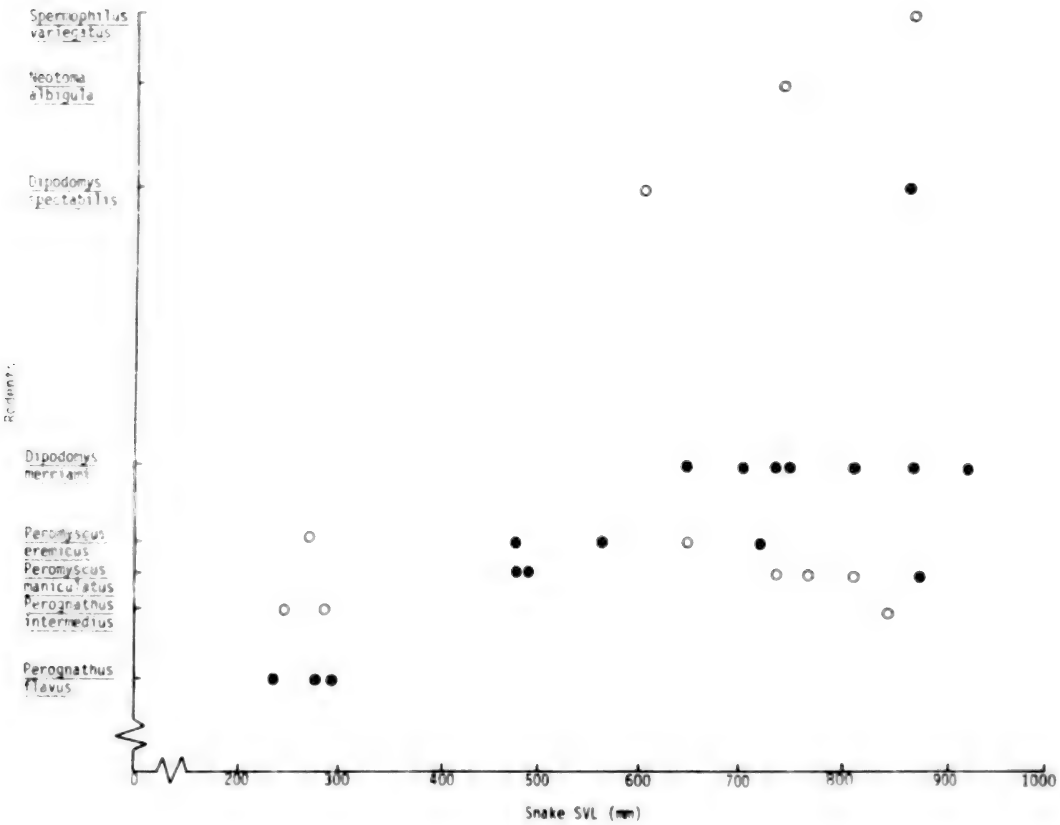

Fig. 11. Results of arena studies with *Crotalus scutulatus* showing acceptance (•) and rejection (◦) of rodents introduced to various-sized snakes. Rodent position on ordinate proportional to average skull breadth, smallest at bottom.

arthropods (insects and millipedes) were taken by young *C. scutulatus*. Damman (1961) suggested that *C. scutulatus* eat more lizards than do *C. atrox* but presented no data to support this statement.

Food supply is the ultimate factor limiting snake populations (Fitch 1949). The presence of a diverse rodent community assures a reliable resource through ecological time. Also, it assures food for snakes of all sizes since certain prey species are taken largely by the young, and others predominately by larger snakes. Considering the fluctuating nature of rodent populations in desert regions (French et al. 1974; Whitford 1976), the optimum strategy of a mammal-eating snake would be that of a species generalist. Within this prey spectrum, the snake can then choose the optimal-sized prey.

In the present study, rodents such as *D. merriami*, *Peromyscus maniculatus*, and *Perognathus flavus* are so abundant and widespread that they are probably not limiting to snakes and therefore there is no competition for them. They may, however, become limiting during periods of extreme population decline. *Crotalus scutulatus*, *C. atrox*, and *P. melanoleucus* are most widespread throughout the various habitats and have the greatest number of rodent prey species available to them. In comparison, *C. molossus* and *E. subocularis* are more restricted to rock habitats and have fewer common rodents available as prey. Birds represent a large proportion (16.7%) of the diets of both these species and they were the only snakes containing *Neotoma albigula*. The inclusion of birds and woodrats in the diet would provide an alternative food resource and reduce competition between these species for the remaining rodent species. Also, Degenhardt and Degenhardt (1965) noted that *E. subocularis* feeds on bats in captivity. Both *E.*

guttata and *E. obsoleta* reportedly prey on bats in nature (Herreid 1961), and it seems likely that *E. subocularis* would also. Inclusion of bats in the diet of *E. subocularis* could reduce competition between this snake and the less scansorial *C. molossus*.

Other vertebrate predators observed in our study area included canids (three species), a felid, procyonids (two species), mustelids (two species), hawks (three species), and the great-horned owl (*Bubo virginianus*). In contrast with the associated predatory mammal and bird species, snake populations occur in much higher concentrations. Fitch (1949), in an area where all predators were abundant, estimated that there were 120 rattlesnakes to each horned owl, 190 to a red-tailed hawk (*Buteo jamaicensis*), and hundreds to a coyote (*Canis latrans*). Factors favoring such concentrations are the relatively small size and the low metabolic rate of snakes allowing subsistence on small food items with long fasts intervening. Also, snakes are relatively long-lived compared with their prey species and may outlive many generations of rodents, and thus survive drastic, periodic changes in prey numbers. Birds and mammals are considerably more vagile than snakes and may respond to reductions of prey populations by moving to new areas, whereas snakes are physiologically better able to weather times of prey scarcity. Snakes, therefore, may have a more continuous influence on prey populations, especially during times of prey scarcity, than those predators whose numbers track the population cycle of prey species.

Snake predation on rodent populations on the San Joaquin Experimental Range had a minor effect on rodent population control (Fitch 1949), but combined with other vertebrate predators, predation accounts for a large part of the annual surplus of rodents. Small mammal populations probably are not predator limited. This has been shown for *Sciurus vulgaris* (Formozov 1933), *Sciurus niger* (Allen 1943), *Rattus norvegicus* (Davis 1951), *Ondatra zibethicus* (Errington 1963), and *Microtus californicus* (Pearson 1966, 1971). Presnall (1950) has similarly concluded that, although rodents are preyed upon intensively, the fluctuations in their numbers are not determined by predation. This applies to such species as the meadow mouse (*Microtus pennsylvanicus*), kangaroo rat (*Dipodomys* sp.), cottontail rabbit (*Sylvilagus floridanus*), and jackrabbit (*Lepus californicus*) (Presnall 1950).

Foraging

Pyke et al. (1977) stated that dietary similarity is central to determination of competitive coexistence of species and that predation, as determined by the foraging behavior of all animals in a community, is the core of its structure. There is a range of possible foraging behaviors determining what prey is eaten, choice of patch type in which to hunt, allocation of time to a patch type, and the patterns and speed of movements. Differences in foraging of the predators and prey in the present study are important to limiting competitive interactions.

Crotalus atrox, *C. scutulatus*, *C. molossus*, and *E. subocularis* are primarily nocturnal, whereas *P. melanoleucus* is diurnal until the onset of summer rains when it becomes crepuscular. Among a group of mammal-eating vertebrates with similar morphologies, noncoincident feeding times could be a mechanism for reducing competition if the prey were also noncoincident in their activity. The heteromyid and cricetid rodents (except *Sigmodon hispidus*) and lagomorphs are primarily nocturnal or crepuscular, whereas the squirrels, *S. hispidus*, birds, and lizards are diurnal or crepuscular in activity. The opportunity to relieve competition through temporal activity differences of predators and prey is present in this community. The food items of *P. melanoleucus* contain crepuscular and diurnal prey including *S. auduboni*, *L. californicus*, *S. spilosoma*, and birds; however, this snake actively searches for prey, often raiding rodent nests (Fitch 1949). As rodent nests are generally underground, it is probable that adult rodents are taken in their burrows as the snake searches for the nest.

In the present study, *S. hispidus* was found only in the mesquite-grassland where *P. melanoleucus* had its highest frequency of occurrence. However, no *S. hispidus* were included in the diet of this snake species. It appears that *P. melanoleucus* is better adapted to foraging for rodents in underground burrows than to hunting *S. hispidus* in grass runways.

The arena tests showed that both *P. melanoleucus* and *E. subocularis* actively pursued their prey about the test arena, whereas *C. atrox*, *C. scutulatus*, and *C. molossus* employed a sit-

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and-wait strategy. The three *Crotalus* species remained motionless in the behavior box until a rodent walked to within striking distance, at which time the snake would strike. A greater number of prey species were found in the diet of the *Crotalus* as compared with the colubrids (Table 7). Random draws, however, from the *Crotalus* samples to adjust for sample size differences between *Crotalus* and the colubrids show no significant differences in the number of items included in diets. The mobility of the colubrids allows the optimal use of suitable habitat patches by hunting only in those patches where the time per item caught is short. The model presented by MacArthur and Pianka (1966) predicts that "pursuers" (i.e., sit-and-wait predators) should show more restricted patch use than searchers where food is dense. The sit-and-wait *Crotalus*, as opposed to the searchers, employ a passive mode of hunting which dictates opportunism and relies on the mobility of the prey, using suitable prey in the proportion that they occur in the environment. There appears to be no differences in successfully procuring prey between the foraging methods employed by the *Crotalus* or colubrids.

Habitat Segregation

The patterns of diversity and interspecific separation of the prey and predatory communities herein described are largely based on habitat segregation. If snakes are competing for food, spatial differences in habitats of sympatric snakes will most effectively reduce competition when these differences coincide with spatial habitat differences of prey species. Schoener (1974) noted that the habitat dimension is usually more important than food type in resource partitioning among reptiles, and concluded that isolation by habitat is more important to terrestrial animals than it is to aquatic animals. In those studies dealing with aquatic or semiaquatic snakes (Carpenter 1952; Fleharty 1967; Mushinsky and Hebrard 1977) the food dimension was found to be more important than habitat. Shine (1977), however, found that for six elapid snake species in Australia, habitat separation played a more prominent role than food type in resource partitioning. These snakes were opportunistic feeders, relatively unselective with respect to prey type or prey size, due to the limited food resources available. He found a preponderance of lizards and frogs in the diets of all species and suggested this is due to the scarcity of small mammals and fish in Australia.

Recently, Maiorana (1978) concluded that spatial dispersion of two plethodontid salamanders widely sympatric in California allowed for their coexistence and regulated population densities. The evidence suggested that burrows were the regulating resource and differences in diet simply an epiphenomenon of the spatial distribution.

The use of food and habitat dimensions are clearly complementary in the snakes studied. There are more food and habitat types available to a snake that it uses. This indicates that a snake exhibits a choice as to the habitat it occupies or prey it eats. Within a habitat type, evolution would favor those snake phenotypes that are better at extracting energy from the more available prey types.

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LIZARD COMMUNITIES

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Temporal and Spatial Resource Partitioning in a Chihuahuan Desert Lizard Community

by

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Abstract

Activity patterns of the lizards in a Chihuahuan Desert creosotebush (*Larrea tridentata*) community were studied by walking fixed transects on a marked grid and recording activity of individual lizards. We found considerable spatial overlap in *Cnemidophorus tigris* and *Holbrookia texana*; however, individuals that overlapped spatially were active at different times. We distinguished five distinct activity patterns in *C. tigris* and *H. texana*, whereas *Uta stansburiana*, *Sceloporus magister*, *Phrynosoma modestum*, *P. cornutum*, and *Crotaphytus wislizenii* were bimodal. Individual activity patterns varied: some were active only in the morning, only in midday, only in the afternoon, morning and afternoon, or all day. Most lizards were active less than 25% of the days of observations. Exceptions were a few large male *H. texana* that were active between 40% and 70% of the days. We suggest that temporal separation of activity reduces intraspecific competition and increases carrying capacity in species for which food is probably not a limiting resource.

Recently there has been considerable interest in resource partitioning in lizard communities (Pianka 1973; Huey and Pianka 1977). Species typically divide resources along three dimensions: food type, habitat, and time (Pianka 1969); most studies have focused on habitat segregation, food size and body size, and daily and seasonal activity patterns (Schoener 1974). These studies, of necessity, have largely ignored differences in activity patterns among individuals in the populations of component species in order to focus on the overall patterns of resource partitioning. Several studies have shown that lizards in climatically varying habitats exhibit interspecific differences in activity periods (Inger 1959; Hillman 1969; Schoener 1970), but studies that have considered activity patterns of individuals have been limited to a single species (Irwin 1965; Simon and Middendorf 1976). Simon and Middendorf (1976) suggested that intraspecific partitioning may reduce competition, increase feeding efficiency, and increase carrying capacity. However, few studies have concentrated on temporal partitioning; Schoener (1974) indicated that temporal partitioning was much less important than food and habitat.

In studies of four sympatric species of Chihuahuan Desert ants, Whitford and Ettershank (1975) and Whitford (1978) showed that temporal partitioning was extremely important in species packing in Chihuahuan Desert ant communities; however, no attempt was made to follow the activity patterns of individual colonies.

Simon and Middendorf (1976) studied individual *Sceloporus jarrovi* and found that most adult activity was in the early morning and most juvenile activity occurred near noon. They also found that individual lizards were active an average of only 2.5 days per week.

In our studies of Chihuahuan Desert lizard communities (Whitford and Creusere 1977), we found seasonal differences in activity patterns of lizard species. We hypothesized that temporal partitioning might be as important in Chihuahuan Desert lizards as it seemed to be in the ants, and that there would be differences in activity patterns between juveniles and adults as suggested by Simon and Middendorf (1976). Therefore, we designed a study of the activity patterns and microhabitat use of individual lizards of the eight species included in a Chihuahuan Desert lizard community. Here we report the results of that study.

Methods and Materials

The study area was on a watershed draining the southeast slopes of Mt. Summerford of the Doña Ana range on the New Mexico State University Ranch, 40 km NNE of Las Cruces, Doña Ana County, New Mexico. The watershed includes an alluvial fan (bajada) dissected by numerous ephemeral watercourses (arroyos) which drain into an ephemeral lake (playa). The soils on the bajada are shallow and sandy and the calcium carbonate deposition layer (caliche) occurs from a few centimeters to over a meter below the surface. The caliche layer is absent in arroyos that have complex soils varying from gravel to loam. The 50-year average precipitation for the area is 225 mm/year; peak rainfall occurs during July and August (Houghton 1972). Summer maximum air temperatures reach 40°C and freezing temperatures are recorded from October through mid-April (data from the Jornada Validation Site Weather Station).

The vegetation is typical of large areas in the northern Chihuahuan Desert. The well-drained areas on the bajada have an essentially monotypic cover of creosotebush, *Larrea tridentata* (23% cover), and all other species contribute about 1% cover. The arroyos are lined with a number of plant species including mesquite, *Prosopis glandulosa* (about 2% cover); tarbush, *Flourensia cernua* (1.5% cover); desert willow, *Chilopsis linearis* (< 1% cover); apache plume, *Fallugia paradoxa* (0.8% cover); and two yuccas, *Yucca elata* (0.2% cover) and *Y. baccata* (0.1% cover). The bajada slope varies from 5% to < 1%.

Studies were conducted on a 160- × 60-m grid bisected by a large arroyo. Nearly all lizards in this area were captured by pitfall traps, noosing, or hand-capture. Each individual was toe-clipped, marked by a tricolored code with enamel paint on its dorsum, and released. Marking had no visible effect on activity patterns and permitted positive field identification of a lizard without subsequent handling. The paint remained intact from 4 to 8 weeks and lizards were repainted when identification became difficult.

A buffer grid was established 60 m on all sides of the main grid. The buffer was used to obtain complete home ranges of animals captured on the primary grid. No pitfall traps were established in the buffer zone. All species except *Cnemidophorus tigris* were either noosed or hand-captured and color-coded. Data for species activity was obtained from the main grid, whereas patterns of activity of individuals included data from both.

A predetermined transect across both grids was walked each hour to record individual activity throughout the day. When a lizard was observed, its color code, location, and time of observation were recorded. Data reported here are based on 100 15-h days of observation from May through October 1975. Climatic data for the periods of observation were obtained from a standard weather station on the site.

When a lizard is "active" on the surface, it spends time searching or waiting for prey alternating with or combined with thermoregulatory behavior. Data obtained from transects provided information only on the type of activity the individual was engaged in at that time. Therefore, we could not divide activity into component behaviors as is possible if individual lizards are followed for extended periods of time. In this study we define "activity" as any behavior occurring on the surface.

We could not use the method of Tanner and Krogh (1974) to evaluate activity. Their method assumes equal probability of sighting for all species. The Jornada is more densely vegetated than the Nevada Test Site studied by Tanner and Krogh (1974), particularly in the arroyos where large perennials block vision. Lizards were often heard but could not be identified before disappearing into shrubs or a burrow.

Behavioral characteristics of species had an effect on the reliability of the data. For example, some sightings of *C. tigris* could not be included in the analysis because the individual could not be identified. *Cnemidophorus tigris* was extremely wary and ran into a burrow if approached too closely. We were unable to approach this species to noose it, and had to rely on can traps for capture and painting. Even with binoculars it was difficult to identify individuals when they were running. There was also a high probability of missing cryptic species such as

Crotaphytus wislizenii and *Phrynosoma modestum*. *Holbrookia texana* was much less wary than *C. tigris* and could often be approached to within 10 m.

To compare species occurring at different densities, we weighted activity by setting the largest sum of all observations for an hour equal to 1.00 and expressing the activity in all other hours as a percentage of that sum.

Spatial overlap was determined by plotting the sightings of individual lizards on maps of the study area. Boundary lines were drawn connecting the outermost sightings for each individual, thereby enclosing the "area of activity." Area overlap between individuals of the same or different species was then taken from these plots. If all sightings of a given lizard were completely within the boundaries of the area of activity of another lizard, the spatial overlap was set at 1.00. Spatial overlap less than 1.00 was set as the percentage of activity area common to both lizards.

Results

Species Activity Patterns

Five species (*Crotaphytus wislizenii*, *Phrynosoma cornutum*, *P. modestum*, *Sceloporus magister*, and *Uta stansburiana*) had bimodal activity patterns. *Cnemidophorus tesselatus* had unimodal activity (in the morning only); *C. tigris* and *Holbrookia texana* were active most of the day (Fig. 1). *Cnemidophorus tesselatus* and *C. tigris* exhibited maximum activity between 0800 and 0900 h. *Sceloporus magister* had its maximum activity at 0730 h and *P. modestum* was most active at 1730 h. *Crotaphytus wislizenii* and *H. texana* exhibited peak activity between 1000 and 1100 h, and *Phrynosoma cornutum* was most active between 0730 and 0930 h. The afternoon peak activity was usually considerably shorter than the morning peak for all species; however, *U. stansburiana* was most active shortly after sunrise (0630 h) and between 1800 and 1900 h on days when cloud cover reduced insolation. Cloud cover appeared to depress the activity of all species except *U. stansburiana*. Nearly all individuals of this species were active on cloudy afternoons but were rarely encountered on clear afternoons. The most frequently observed lizard species were *H. texana* and *C. tigris*, which were also the most abundant (Whitford and Creusere 1977). We usually saw more males than females (Fig. 1).

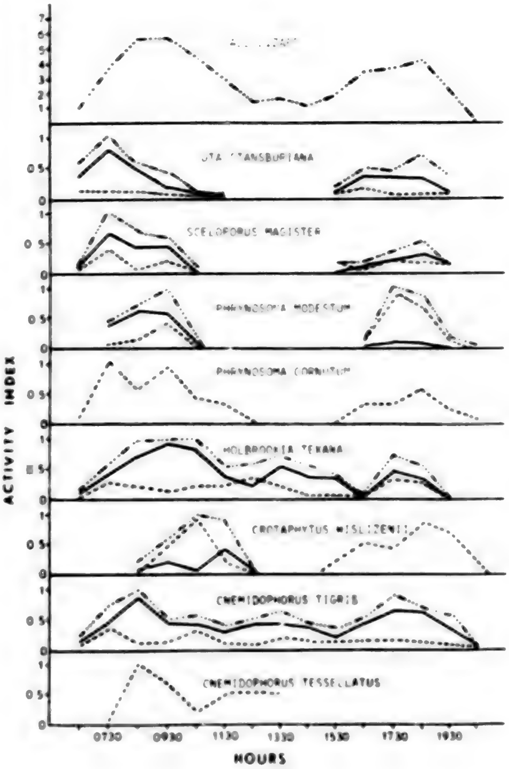

Fig. 1. Activity patterns of the lizards in a Chihuahuan Desert community. The activity index was derived by setting the largest number of observations equal to 1.00 and expressing the number of observations for all other hours as a fraction of 1.00. Dashed lines represent activity of females, solid lines the activity of males, and dot-dash lines the sum of the activity of all individuals seen, some of which were not sexed.

Several hundred hours of observations yielded only 11 interspecific encounters. Seven of these resulted in both individuals fleeing a short distance, then immediately continuing their search for food. Three encounters between male *U. stansburiana* and *C. tigris* of both sexes resulted in the larger *C. tigris* ignoring the bobbing of the former and continuing its search for termites. The only successful interspecific defense of an area occurred when a female *P. cornutum* charged and pursued a large male *C. tigris* that had wandered into her territory while she was depositing eggs.

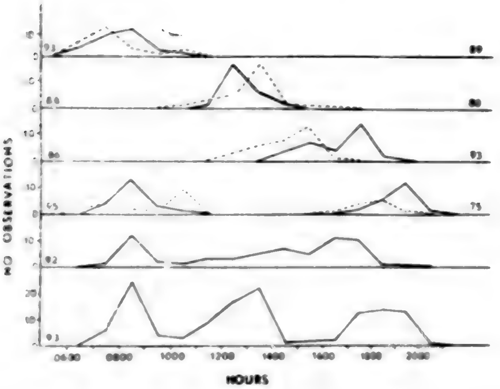

Fig. 2. Activity of the 10 most frequently encountered *Cnemidophorus tigris*. Dashed lines represent females, solid lines males. Snout-vent (S-V) lengths of males are on the left, S-V lengths of females on the right.

Individual Activity Patterns

Individuals in each species consistently maintained a preferred time of activity that made up only a portion of the total activity for the species. Within the populations of *C. tigris* and *H. texana*, we found five main patterns of daily activity: (1) early morning only, (2) midday only, (3) afternoon only, (4) both early morning and late afternoon, and (5) activity throughout most of the day (Figs. 2 and 3). The activity patterns of *U. stansburiana* are typical of species having a bimodal activity pattern. Individual lizards of bimodal species showed three patterns of activity: (1) morning only, (2) afternoons only, and (3) both morning and afternoon (Fig. 4). *Cnemidophorus tesselatus* was restricted to morning and midday activity on the study site but was observed to be active throughout the day in adjacent areas.

We made sufficient repeated observations on 30 of the 61 marked *C. tigris* to provide reliable estimates of individual activity patterns. Eight exhibited early morning activity, five were active only at midday, seven were active only in the afternoon, seven exhibited both morning and late afternoon activity, and three were active throughout most of the day. However, none of these individuals were seen on more than 25% of the days and most were seen only 10-15% of the days. The patterns of 10 of the most frequently encountered *C. tigris* are shown in Fig. 2. Of the 13 *H. texana*, 3 were active only in the mornings, 2 were active only in the afternoon, 3 were bimodal, and 5 were active throughout the day (Fig. 3). Three of the large male *H. texana* were seen on 60-70% of the days but the remainder were only seen on 15-40% of the days. Of the 13 *U. stansburiana*,

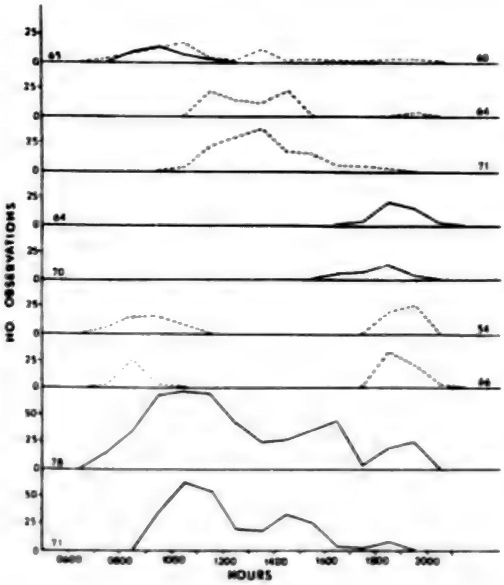

Fig. 3. Activity patterns of the 10 most frequently encountered *Holbrookia texana*. Dashed lines represent females, solid lines males. Snout-vent (S-V) lengths of males are on the left, S-V lengths of females on the right.

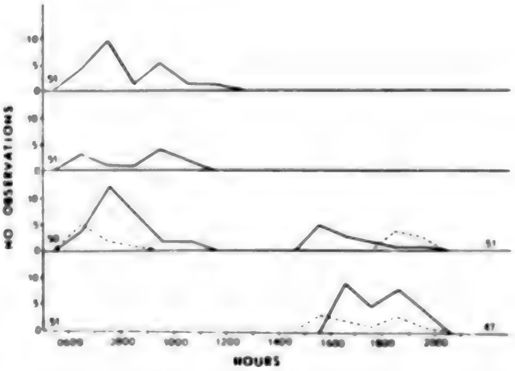

Fig. 4. Activity patterns of six *Uta stansburiana* selected to show the different activity patterns discussed in the text. Dashed lines represent females, solid lines males. Snout-vent (S-V) lengths of males are on the left, S-V lengths of females on the right.

5 were active only in the morning, 4 were active only in the afternoon, and 4 were bimodal (Fig. 4). The three *P. modestum* and three *S. magister* were bimodal. Three *P. cornutum* were active only in the morning, one was active only in the afternoon, and one was bimodal. Two *C. tesselatus* were morning active only and one was active only at midday. Of the four *C. wislizenii*, two were bimodal, one was morning active, and one was afternoon active.

In previous studies (Whitford and Creusere 1977) we noted that the number of individuals observed hourly seldom exceeded 25% of the population based on mark-recapture estimates. When we increased the number of observers to six and walked a 60-m-wide transect across the site, we improved only slightly; 35% of the estimated population was observed. Previous pitfall trap data for 1970–74 indicated that many individuals were captured several times in one area followed by several weeks without recapture before being taken again in that area. We initially assumed that these lizards foraged in adjacent areas for a period of time before returning to the trapping grid. However, frequent sightings of individuals were followed by periods with no sightings on either the grid or buffer zone, which suggests these animals may have been aestivating. Some individuals of all species remained active throughout the summer.

The individuals that had short periods of activity were feeding during most of that period. Lizards with more extended activity periods fed in short spurts throughout the activity period, spending the remainder of the time at rest on the surface.

Spatial Patterns

To adequately interpret the temporal activity patterns of individual lizards, it is necessary to examine their spatial distribution. There was little spatial overlap in the species occurring at low densities, and here we present data only for *C. tigris* and *H. texana*.

The overlap of male and female *C. tigris* was almost complete (Fig. 5). Of the area occupied by males, 47% was used by only one male, 37% by two, 11% by three, and 5% by four. The average number of individuals using a given point within all the male activity areas was 1.7. Maximum overlap values for male *C. tigris* are as follows: 1.00 overlap with at least one other male, 0.90 with at least two other males, and 0.50 with three or four other males (i.e., one male's activity area was completely contained in the areas of other males, 90% of one male's activity area fell into areas used by two or more other males, and 50% of one male's activity area was used by at least three other males).

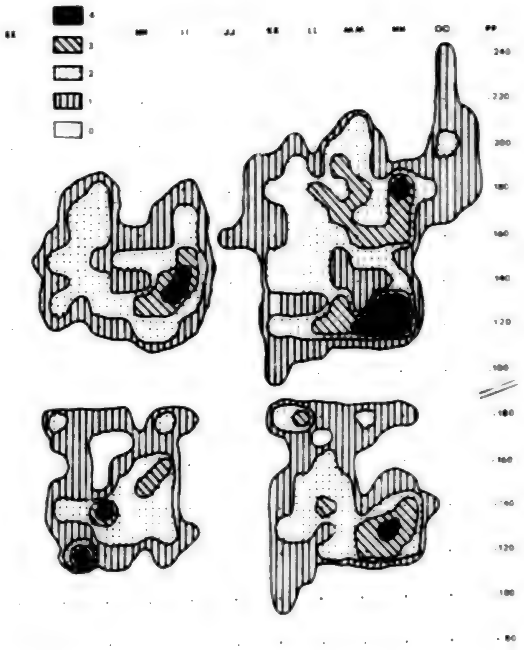

Fig. 5. Spatial overlap in *Cnemidophorus tigris*. The upper plots are for males and the lower plots for females. Different patterned areas indicate use by zero to four individuals of the same sex. Grid points are 20 m apart.

Female use of space was similar: 51% of female activity areas was used by only one, 35% by two, 11% by three, and 4% by four. The average number of females using a given part of an activity area was 1.7 – the same as for males. Maximum overlap for female activity areas was 0.81 with one or more other females, 0.45 with two or more others, and 0.45 with three or four others.

Among male *H. texana*, the maximum observed overlap was 0.62 with at least one other male, 0.50 with two or more others, and none overlapped with three others. There was virtually no overlap in *H. texana* females; the maximum overlap for any female activity area was 0.12 with one other.

In spite of overlaps, we almost never observed more than one individual of a species in proximity to another of the same species.

During the few weeks when both adults and juveniles were active, the adults tended to remain in the vicinity of denser vegetation and juveniles appeared to be relegated to more open vegetation. For example, adult *H. texana* were usually found in large arroyos having >1 m^2 of open stream bed, some rocks, and dense clumps of apache plume at the edge. Juvenile *H. texana* were found in the open upland areas of creosotebush until the adults ceased activity late in the season. The juveniles then migrated to the arroyos.

Discussion

The most intriguing result of these studies is that in the most numerous species individual lizards exhibited consistent but abbreviated patterns of activity. Many individuals in the population do not overlap temporally although these same individuals may overlap spatially. This temporal separation reduces intraspecific competition and increases carrying capacity probably by increasing feeding efficiency. This seems particularly likely in *C. tigris*, which occurs at densities of 30–40/ha (Whitford and Creusere 1977) and which have home ranges of about 0.57 ha (range 0.1–2.4 ha) in this study. *Cnemidophorus tigris* feed primarily on termites (Pianka 1970) by rooting through accumulations of leaf litter. Although a morning feeder would disturb the termites and remove a small number, the subterranean galleries of the termites would be left undisturbed. If the litter is in a shaded, temperature-moderated area, the termites will reenter within a few hours (Johnson and Whitford 1975; W. G. Whitford, personal observation). Thus, individual lizards active at different times of the day could feed in the same location. Even at densities of 30–40/ha, *C. tigris* is not likely to deplete the termite population which we estimate conservatively to exceed 1,200/m^2 (Johnson and Whitford 1975) With a food resource as large and temporally flexible as termites, *C. tigris* can exist at high densities avoiding intraspecific competition by utilizing the same space at different times of the day.

Simon and Middendorf (1976) presented the only recorded example of spatial and temporal overlap in a single species of lizard and stated that little overlap has been described in any taxon. Here we document temporal and spatial overlap in *C. tigris* and *H. texana*. We suggest that such overlap may be the rule rather than the exception, particularly in species that achieve high densities. There are many species of organisms that use extremely abundant food resources and that occur at densities that should result in considerable intraspecific competition because of spatial overlap. Intraspecific interactions are energy expensive and, if agonistic, can be damaging. There appears to be remarkable lack of intraspecific agonistic behavior in harvester ants (Whitford 1976), and in *C. tigris* and *H. texana* as documented in this study. It seems likely that temporal separation could be behaviorally established early in a season and maintained throughout the season.

Spatial overlap of a male and female in sexually reproducing species is expected, but spatial overlap of several males is not. The relation between lizard body size and extent of activity suggests the behavioral establishment of a temporal hierarchy. In *H. texana*, the largest lizards exhibited the all-day pattern of activity. The smaller lizards had the more temporally restricted activity pattern. This could be interpreted as dominant-subordinate interaction; the subordinate is relegated to less favorable foraging times. The peak activity of ground and litter arthropods is in the early morning and evening when temperatures near the ground are more favorable for their activity (W. G. Whitford, unpublished data). Larger lizards may have to spend more time active on the surface to maintain body temperatures at preferred levels for digestion and other physiological processes, and they may require a longer time to fill their stomachs. This need for an extended feeding–digestion period seems to be a reasonable explanation for the body size–activity pattern in *H. texana*.

It is apparent from this study that individual lizards are not surface active every day; the data suggest that most are active about 2 days per week or less. Simon and Middendorf (1976) found that *Sceloporus jarrovi* were active on the average only 2.5 days per week. Even allowing for large errors in our data due to the limitations of the walking transect technique, we can state with confidence that individual lizards were active less than 50% of the time with the few exceptions noted in *H. texana*. Considering a pattern of surface activity that is less frequent than daily and the reduced diel activity patterns of individual lizards, it is apparent that temporal partitioning is much more important than previously thought (e.g., Schoener 1974) and deserves further investigation to see if this results in a partitioning of food resources.

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Use of Cave Resources by a Lizard Community

by

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Abstract

A community of three lizard species exploits the resources of a system of caves at Puerto Marquez, Guerrero, Mexico. The caves provide a stable, low-temperature, high humidity environment with variable and sparse food resources. *Anolis taylori*, *Phyllodactylus lanei*, and *Lepidophyma smithi* differ in the degree to which they utilize the cave resources. These differences are apparent in activity pattern, body temperature, evaporative water loss, and diet. Adaptations for cavernicolous life involve absence of a diel activity cycle, absence of thermoregulatory activity, low resistance to water loss, and a generalized diet that, at Puerto Marquez, includes decaying fruit and probably carrion

Cave communities are distinctive in that they contain no photosynthetic autotrophs (Barr 1967, 1968; Poulson and White 1969). The food web within a cave is based on detritus which is transported from the outside by flooding or animal movements. Cavernicolous animals must therefore be adapted to food resources that are often scarce, of little nutritive value, or sporadic in availability. As a consequence of these energetic restrictions, the subterranean community is greatly simplified compared to its epigean counterpart, both in terms of lower species richness and standing crop biomass. Caves are buffers to changes in the outside climate. Temperature is stabilized at very near the average yearly epigean temperature, and humidity is high and stable. The magnitude and lag of fluctuations depend on how open the system is, which in turn depends on the size, number, and exposure of entrances, and the distance from the entrances (Poulson 1964).

Most cavernicolous vertebrates are facultative although a small number of salamanders and fishes are obligate cave inhabitants. Few lizards are associated with cave communities. Xantusiid lizards of the genus *Lepidophyma* have been found in caves (Walker 1955; Smith and Alvarez del Toro 1977) but little is known of the biology of these species.

I report here on the use of a cave system in southern Mexico by three species of lizards: *Anolis taylori*, *Phyllodactylus lanei*, and *Lepidophyma smithi*. Different degrees of adaptation to cavernicolous life are shown in comparisons of the activity patterns, thermoregulation, water loss, and diet of these species.

Materials and Methods

Observations were made in August 1973, July 1974, and January and November 1976, at a site 2 km west of Puerto Marquez, Guerrero, Mexico. Caves in this region are formed by large granitic boulders that are piled in ravines draining steep hillsides. The boulder aggregations produce a system of caves with multiple entrances and extensive twilight zones grading to complete darkness in the deeper recesses (Fig. 1). This unique structure permits input of detritus and provides access to animals over a large surrounding area. The surface vegetation is a semideciduous tropical forest. Average monthly temperatures range from 26° to 29°C and average annual rainfall is 1,400 mm, nearly all of which falls between May and October (Instituto de Geographica, Universidad Nacional Autonoma de Mexico).

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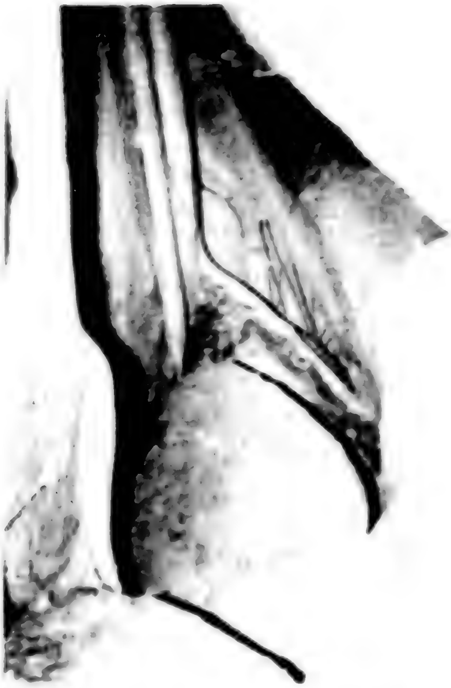

Fig. 1. Interior view of a cave at Puerto Marquez, Guerrero, Mexico. Roots of fig trees, *Ficus petiolaris*, entwine boulders and penetrate to soil below. The boulder in the lower center of the photograph is about 1 m in diameter.

Measurements of temperature and humidity in the cave twilight zone and forest floor environments were made with a sling psychrometer held 1 m above the substrate. Lizard body temperatures were measured within seconds of capture by cloacal insertion of a Schultheis rapid registering mercury thermometer. All thermometers were calibrated against a National Bureau of Standards certified mercury thermometer; humidities were calculated from List (1949). Lizard activity was determined by direct observation and trapping (Mautz and Lopez-Forment 1978). Evaporative water loss was measured in the field by direct weighing. Lizards were placed in plastic boxes 10 cm on a side with screen floors over a layer of mineral oil. The boxes were roofed with additional screen to permit equilibration with the stabilized microclimate of the cave. Lizards were weighed to 0.01 g every 24 h. Fecal masses were collected and stored under oil for determination of water content by the method of Minnich and Shoemaker (1972). Water loss data from animals that defecated were discarded. A series of animals were collected for analysis of gut contents.

Results

The diel variation in temperature and vapor density deficit is plotted in Fig. 2 for sites both inside and outside the caves during wet and dry seasons. Vapor density deficit is the difference between the concentration of water vapor in the air and the saturation concentration of water vapor at the air temperature. It is a measure of the evaporating potential of the air; high values of vapor density deficit represent a high evaporation potential. During both wet and dry seasons, the cave environments maintained a steady and low temperature and vapor density deficit, cycling between 24° and 27° C and 2 to 5 g m^{-3}, respectively. Organisms in the cave environment enjoy the benefits of a reduced evaporation potential, but must contend with a temperature regime which, while stable, is relatively low.

The three species of lizards differ markedly in the time spent and the activities performed in the caves. The iguanid, *Anolis taylori*, moves into the caves shortly before sunset and is inactive through the night. These lizards cling to open vertical surfaces and do not seek the close confines provided by thin crevices within the caves. This behavior may minimize the risk of predation by large scorpions and amblypygids, which frequent fissures in the cave walls. The anoles do not penetrate to the dark zone of the caves at any time during the night. At dawn they move to the surface to forage and bask. The gekkonid, *Phyllodactylus lanei*, can be found on the walls and in crevices within caves by night or day; it is also found on the surface outside of caves from shortly after sunset to midnight. Ten specimens collected from the surface all had food in their stomachs. Four of these contained intact arthropods, indicating that the lizards forage on the surface at this time. The xantusiid, *Lepidophyma smithi*, is found only within caves. Individuals were located by night and day within crevices and on the walls, and they were captured in equal frequencies by day or night in traps baited with fish (Mautz and Lopez-Forment 1978). *Lepidophyma smithi*

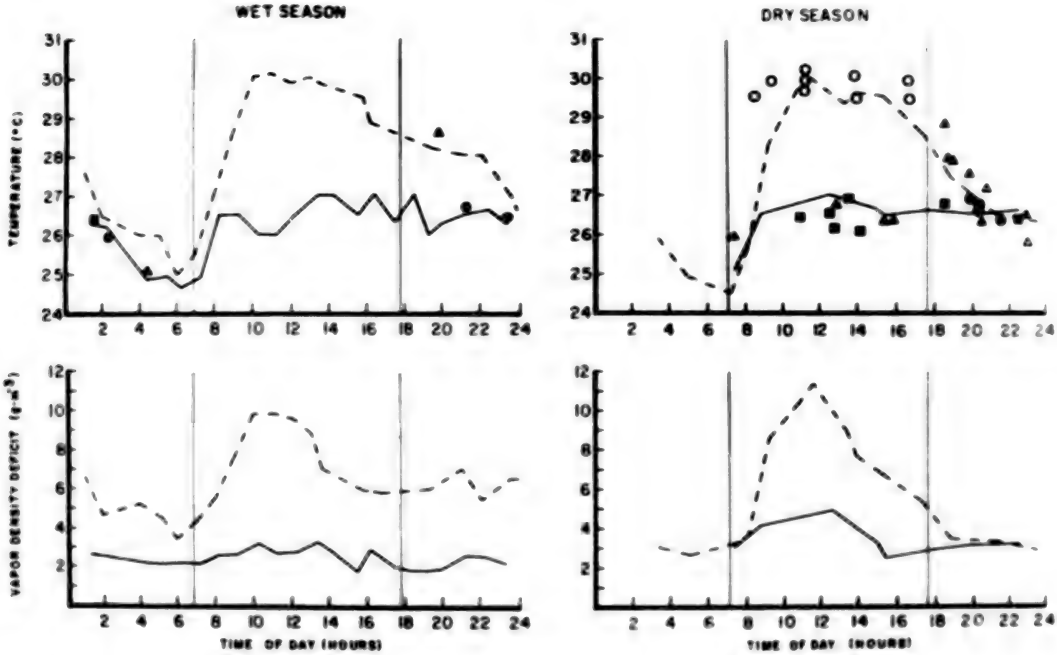

Fig. 2. Microclimate variation and lizard body temperatures at Puerto Marquez, Guerrero, Mexico. Dashed lines are air temperature and vapor density deficit outside of caves, solid lines are inside caves, open symbols are lizards outside caves, solid symbols are lizards inside caves; circles (,●), *Anolis taylori*; triangles (, ▲), *Phyllodactylus lanei*; and squares (■), *Lepidophyma smithi*. Thin vertical lines indicate time of sunrise and sunset. Wet season data were collected 7–8 July 1974, and dry season data were collected 28–29 November 1976.

thus appears to forage without a diel activity cycle.

Temporal and spatial differences in the activity of these lizard species are correlated with their body temperatures (Fig. 2). By day, *A. taylori* frequents tree trunk and ground microhabitats where it basks in the early morning and late afternoon, elevating its body temperature to 30°C. During midday, the air temperature is sufficiently high for the lizards to maintain activity temperatures without basking. Shortly before sunset the lizards move into the openings of the caves and assume sleeping positions; their body temperatures then closely approximate cave air temperature. *Phyllodactylus lanei* exhibits two kinds of body temperature cycle depending on whether the animals emerge or remain in caves in the evening. Animals remaining in caves have body temperatures equal to cave air temperature. Emergent animals achieve evening body temperatures higher than outside air temperature by heat conduction from boulder surfaces warmed earlier by sunlight. Later at night large areas of the boulder surfaces exposed to the night sky may cool by radiant heat loss to levels below air temperature. The low body temperature of a *P. lanei* at 2300 h on 29 November (dry season data, Fig. 2) is probably a result of contact with an exposed boulder surface from which it was collected. Since *L. smithi* do not leave the caves, their body temperatures consistently equal cave air temperature.

Rates of water loss in milligrams H_2O g per h of the three lizard species (Table 1) do not differ significantly ($F = 0.48$); however, differences in the body weight and activity of the animals obscure physiological differences in their resistance to water loss. *Lepidophyma smithi* is nearly three times as massive as the other species, but its surface area, estimated by $SA = 10 \cdot W^{0.67}$ (Benedict 1932), is less than twice that of the others. Thus the conductance of water vapor for *L. smithi*, expressed per unit of surface area instead of per unit mass, is higher. The reciprocal of conductance, resistance, will be correspon-

Table 1. *Evaporative and excretory water loss of* Anolis taylori, Phyllodactylus lanei, *and* Lepidophyma smithi. *Values are means ± standard errors.*

	Body weight		Evaporative water loss		Water content of excreta	
Species	No. of specimens	g	No. of specimens	mg g per h	No. of specimens	% wet weight
Anolis taylori	7	6.9 ± 0.73	7	1.01 ± 0.08	6	70 ± 3
Phyllodactylus lanei	5	5.9 ± 0.03	5	1.26 ± 0.34	1	67
Lepidophyma smithi	5	17.5 ± 2.41	5	1.12 ± 0.08	13	65 ± 2

dingly lower than that for the other species. Therefore, *L. smithi*, the species with the strongest affinity for caves, has the lowest resistance to water loss. Furthermore, there is great variation in activity among the lizard species. *Lepidophyma smithi* is a sedentary lizard which rarely moves from perch sites within caves. Emerging *P. lanei* are slightly more active; individuals typically make short excursions interspersed by long periods of inactivity. In contrast, *A. taylori* makes short rapid movements over boulders and tree trunks with considerable frequency. These activity patterns were also reflected in the behavior of the animals during water loss measurements. *Lepidophyma smithi* and *P. lanei* remained motionless whereas *A. taylori* often jumped at the sides of the containers. Animal activity is rarely controlled in studies of water loss, but it does exert a marked effect on evaporation (Gans et al. 1968; Dmi'el 1972; Mautz 1980). The activity of the *A. taylori* probably elevated its water loss rates above resting levels; it is likely that physiological resistance to water vapor flux at rest is higher in this species. The other avenue of water loss is excretion and all three species appear to lose the same proportion of water in feces and urates (Table 1).

The diets of *A. taylori* and *P. lanei* consist of a variety of small arthropods, but *L. smithi* feeds almost entirely on *Ficus* fruit that falls or washes into the caves.

Discussion

Cavernicolous organisms inhabit an environment of darkness, low temperature, high humidity, and biotic simplicity. Differences in the extent to which these organisms occupy caves and are restricted to them are reflected in a gradation of adaptations to the cave environment. Obligatory cave existence is not known among lizards, but species that are secretive or nocturnal possess some of the appropriate adaptations – characteristics which are "protoadaptations" for cavernicolous life. These species are able to utilize caves to different degrees. Lizards found in the caves at Puerto Marquez exemplify such a gradation in adaptations and, in correspondence, a gradation in involvement in the cave community. In the absence of physiological tolerance to low temperature, heliothermic iguanids like *A. taylori* will be excluded from cave habitats except during the inactive phase of their daily cycle. Some other *Anolis* species are not heliotherms and their body temperatures passively follow air temperature (Hertz 1974; Huey 1974; Huey and Webster 1976). Thermal constraints alone are insufficient to exclude such eurythermic iguanids from caves. Gekkonids and xantusiids have low activity temperatures (Brattstrom 1965; Mautz and Case 1974; Pianka and Pianka 1976). These are compatible with the warmer caves in tropical and subtropical climates. *Phyllodactylus lanei* achieves elevated body temperatures during the brief interval of evening emergence. This may be an important component of the thermal biology of these animals in that it enhances digestion at a time when the lizards are foraging (Regal 1966). *Phyllodactylus lanei* and *L. smithi* exhibit no thermal or activity characteristics peculiar to their families except for the apparent lack of a diel activity cycle in *L. smithi*. The temperate xantusiids, *Xantusia henshawi*, *Xantusia vigilis*, and *Klauberina riversiana*, possess diel activity cycles (La Pointe 1967; Regal 1967; Lee 1974; Mautz and Case 1974). The lack of rhythmicity in *L. smithi* may not be unique, as no one has studied the activity of other *Lepidophyma* species in lowland tropical climates where tem-

peratures may be suitable for nocturnal and diurnal activity.

Environmental determinants of evaporative water loss also differ between cave and epigean habitats. Lower temperature and water vapor density deficit in the caves produce an environment in which evaporation will be reduced. If other factors influencing the water budget of lizards were equal, one would expect a reduced physiological resistance to evaporation in cavernicolous species, which would be reflected by high water loss rates for these animals. Other factors were not equal among the three species studied and physiological resistance to evaporation was not directly measured, but a number of inferences can be drawn from the evaporative water loss measurements. The rates at which the tissues of the three species desiccate by evaporation (mg/g per h), the water content of excreta, and thus the rate at which lizards must replenish lost water are equal. It appears that the sources of water for these lizards, largely water in food and freestanding drinking water, are similar. Differences in the resistance to water loss of these species are implied by differences in body size and activity. *Lepidophyma smithi* is a much more massive animal with a correspondingly lower surface to mass ratio, and the resistance to water loss across its surface must be much reduced to produce a desiccation rate equivalent to the other smaller species. *Anolis taylori* and *P. lanei* are similar in size but differ markedly in activity. The equivalence of desiccation rates in these species implies a reduced resistance for the sedentary gekkonid compared to the active iguanid. It appears that physiological resistance to water loss may be adjusted to compensate for the differing effects of body size, activity, and environment.

Probably the greatest challenge to lizards inhabiting caves is the scarcity of quality food resources. At Puerto Marquez, *A. taylori* does not forage inside the caves, and a large proportion of the population of *P. lanei* also forages on the surface. The omnivorous diet of *L. smithi* admirably suits these lizards to life entirely within these caves. They find the bulk of their food among the detritus that falls and washes into the caves and supplement this diet with occasional arthropod prey and probably carrion. Nothing is known of the diet of other *Lepidophyma* species, but another large xantusiid, *Klauberina riversiana*, has a generalized, omnivorous diet (Knowlton 1949; Schwenkmeyer 1949). It is therefore likely that other large species of *Lepidophyma* are at least partially herbivorous.

Many lizards may be protoadapted for occupying caves because they are tolerant of low temperature, low light levels, and scarce or nutrient-poor food. *Anolis taylori* is ill equipped for these typical cave conditions and consequently it uses caves only as a nocturnal retreat. *Phyllodactylus lanei* is better adapted for living in caves but emerges to forage at night. *Lepidophyma smithi* can remain within caves continuously although it probably is not restricted to caves. The adaptations of the latter two species are effective in suitable epigean habitats as well, and are also present in other nocturnal and secretive members of their families which do not live in caves.

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Structure and Composition of Mojave Desert Reptile Communities Determined with a Removal Method

by

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Abstract

Species diversity, relative abundance, and biomass were determined by a removal method for communities of diurnal reptiles (lizards and tortoises) in creosote-shrub habitat in the western Mojave Desert, California. Collecting on 2 consecutive days (3 h in late morning) proved effective in sampling the fauna. Four to six species occurred at each site; the species diversity indices varied little between sites. Three species of lizards made up 83% of the individuals in the sample: *Callisaurus draconoides*, *Cnemidophorus tigris*, and *Uta stansburiana*. The desert tortoise, *Gopherus agassizii*, constituted 80% of the estimated biomass. Of the remaining biomass, 84% was contributed by *Cnemidophorus tigris*, *Callisaurus draconoides*, and *Phrynosoma platyrhinos*.

Descriptions of reptile communities should include measures of species diversity, abundance, and estimated biomass because all of these variables help to delineate the importance of certain components and indicate relations in communities. For example, *Gopherus* was numerically uncommon in the present study but because of its large size it is an energetically important herbivore in creosote-shrub habitat.

No sympatric congeners occurred in the study sites. All of the reptiles appeared to be broadly different in food habits or microhabitat, or both, which reduces interspecific competition.

Most research on North American desert reptiles has focused on autecological studies, e.g., the biology of *Sceloporus magister* (Tinkle 1976); *Crotaphytus wislizenii* (Turner et al. 1969*a*; Tanner and Krogh 1974; Parker and Pianka 1976); *Phrynosoma platyrhinos* (Medica et al. 1973; Pianka and Parker 1975); *Callisaurus draconoides* (Kay 1970; Pianka and Parker 1972; Tanner and Krogh 1975); *Cnemidophorus tigris* (Medica 1967; Turner et al. 1969*b*; Pianka 1970; Parker 1972); *Uta stansburiana* (Tinkle 1967; Turner et al. 1970); *Dipsosaurus dorsalis* (Krekorian 1977); and *Gopherus agassizii* (Engberg et al. 1976). These studies provide important comparative data on single species.

Studies on sympatric species of desert lizards are few but explore important aspects of community structure. Pianka (1967, 1973, 1975) investigated species diversity and niche relations of North American desert lizards. Whitford and Creusere (1977) and Creusere and Whitford (this volume) reported on temporal changes in a Chihuahuan Desert lizard community.

The present study employed a removal method to analyze the species diversity, density, and biomass of diurnal reptiles in creosote-shrub habitats in the Mojave Desert. These measures were used to better define the structure and composition of desert reptile communities.

Materials and Methods

In 1974 and 1975, field studies were conducted at four undisturbed localities in San

Table 1. *Lizards and tortoises taken on 2 days (6 man-hours/ha) on 2-ha sites, western Mojave Desert, California.*

Site	Number of species	Number of individuals	Species diversity index	Total biomass (g/2 ha)	Lizard biomass (g/2 ha)
Barstow					
A	6	57	1.39	3,189	643
D	5	60	1.26	4,597	737
Stoddard Wells					
E	5	54	1.27	490	490
G	5	46	1.48	509	509
Anderson Valley					
K	6	26	1.59	1,480	480
L	5	31	1.46	9,023	348
Johnson Valley					
M	4	46	0.94	474	474
N	6	53	1.1[illegible]	1,080	580

Bernardino County, California, in the upland portion of the western Mojave Desert. Two sites of 2 ha each were sampled at the four localities, for a total sample area of 16 ha. All study sites were between 740 and 1,100 m in elevation and were dominated by creosotebush (*Larrea tridentata*, $\bar{x}$ = 240 shrubs per ha, range 153–328). The study sites are described elsewhere (Bury et al. 1977).

The rationale for, and development of, the removal sampling techniques to estimate population size were described by Zippin (1956, 1958) and Delany (1974). I found that this method was an effective sampling technique for measuring diurnal reptile populations (Busack and Bury 1974; Bury et al. 1977). In earlier work, I expressed population size as the total sample collected, and I follow this method here to facilitate comparisons. Measures of species diversity, abundance, and biomass were calculated from the total of all animals taken. A similar standardized procedure was used to study desert rodents (Brown 1973, 1975; Brown and Lieberman 1973).

The removal method consisted of systematic, repeated search of established quadrats (100 × 200 m); collection was by shooting with elastic bands or .22 dust shot, and by hand-capture. Two collectors sampled halves of the 2-ha sites simultaneously (from 0900 to 1200 h) and exchanged halves daily to reduce collecting bias. Searching was done from late April to early June, the peak periods of surface activity for diurnal reptiles in the Mojave Desert.

The minimum sampling period was 3 h/day for 2 days. Comparisons were made on data obtained from the first 2 days of sampling at all eight sites. A third sampling day of 2 h was obtained at six of these sites. These data were used in the discussion of sampling methods.

All animals were removed from the quadrats, sexed, measured, and weighed (to the nearest 1 g or, for small reptiles, 0.1 g). Animals killed were prepared as museum specimens. Protected forms (*Gopherus*, *Phrynosoma*, *Crotaphytus*) were measured and released alive at the place of capture.

Three snakes (*Pituophis*, 450 g; *Masticophis*, 250 g; and *Sonora*, 8 g) were found on the sites. They were not included in the data analysis. Other sampling techniques are needed to accurately estimate the number of snakes present. In the results and discussion that follow, "reptiles" refers to lizards and tortoises only.

Results of Removal Sampling

Use of the removal sampling technique provided estimates of relative occurrence (species diversity), abundance (number per unit area), and biomass (weight per unit area) (Table 1). The majority of individual reptiles were taken on the first day (Fig. 1, Fig. 2*a*). The average

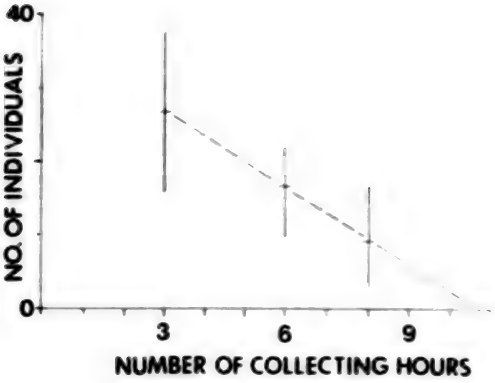

Fig. 1. Number of individuals of diurnal lizards and tortoises removed on 3 successive days from Mojave Desert sites (N = 5). Vertical bars are ranges and horizontal bars are means. Dashed line is fitted by eye.

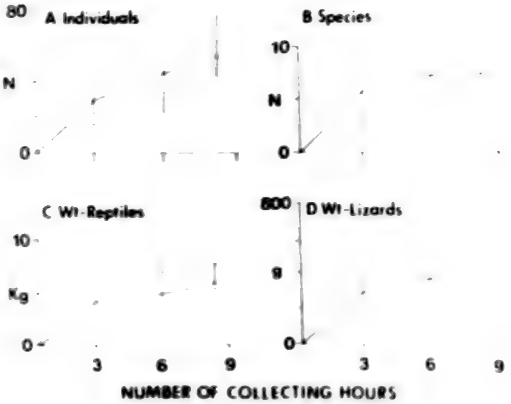

Fig. 2. Cumulative totals of (a) numbers of individuals, (b) numbers of species, (c) weights of diurnal lizards and tortoises, and (d) weights of diurnal lizards alone, obtained over 3 days (3:3:2 h periods) on eight 2-ha sites in the Mojave Desert. Vertical bars are ranges and solid lines connect means.

number of reptiles obtained per day declined steadily from Day 1 to Day 3.

The average number of species per site were Day 1, 5.4; Day 2, 4.0; and Day 3, 2.6. New species were added on only two of the eight sites on the second day of sampling (one *Dipsosaurus dorsalis* at site N, one *Callisaurus draconoides* at site E) (Fig. 2*b*). No additions were made on the third day. Thus the removal method revealed almost all the resident diurnal reptile species in two sampling days. There may be some uncommon or peripheral species that will be found only with long searches, but the species composition of desert diurnal reptiles evidently can be effectively determined in 2 days by the removal technique.

The cumulative weights of reptiles captured were not noticeably increased with further hours of collecting (Fig. 2*c*). This was principally due to the large weights of desert tortoises (*Gopherus agassizii*), which were generally found on Day 1 because they were conspicuous and usually easy to locate if burrows were carefully searched. Similarly, the greatest lizard biomass was recorded on Day 1 (Fig. 2*d*).

Species Diversity

The number of species collected on the first 2 days at each of the eight sites varied from four to six ($\bar{x} = 5.3$). The Shannon and Weaver (1963) Index was used to compare species diversity. Little difference between the sites was found; index values were from 0.94 to 1.59 (Table 1).

Callisaurus draconoides, *Cnemidophorus tigris*, and *Uta stansburiana* occurred on all study sites (Table 2). *Phrynosoma platyrhinos* was found on six sites. Both *Sceloporus magister* and *Dipsosaurus dorsalis* were recorded on only one quadrat; the populations of these relatively heavy-bodied lizards were lower on the study sites than in other habitats. The sites had few suitable habitats for those lizards: few or no trees and little sandy soil. I found *Sceloporus magister* at Stoddard Wells, where there were a few scattered Joshua trees (*Yucca brevifolia*). The one *Dipsosaurus* I found was in Johnson Valley, where some sandy areas occurred.

Urosaurus graciosus, a shrub- or tree-dwelling form, was not found in the study areas, but this species frequents creosote habitat elsewhere. *Coleonyx variegatus* probably was present, but the nocturnal lizard fauna was not sampled. *Xantusia vigilis* also probably occurred at many sites, but special collecting efforts (raking through surface debris) are needed to find these lizards.

Composition of Herpetofauna

Three species of lizards made up 83% of the reptiles sampled (Table 2); *Callisaurus draco-*

Table 2. *Number and percentage of individuals taken on 2 days (6 man-hours/ha) at eight 2-ha sites, Mojave Desert, California. Figures in italics are the percentage of individuals at each site.*

	Barstow		Stoddard Wells		Anderson Valley		Johnson Valley		
Species	A	D	E	G	K	L	M	N	Total
Callisaurus draconoides	5	28	1	10	6	8	31	33	122
	8.8	*46.7*	*1.8*	*21.7*	*23.1*	*25.8*	*67.4*	*62.3*	*32.7*
Cnemidophorus tigris	27	18	19	8	9	7	9	8	105
	47.4	*30.0*	*35.2*	*17.4*	*34.6*	*22.6*	*19.6*	*15.1*	*28.2*
Uta stansburiana	15	8	19	15	5	10	3	8	83
	26.3	*13.3*	*35.2*	*32.6*	*19.2*	*32.3*	*6.5*	*15.1*	*22.3*
Phrynosoma platyrhinos	5	–	13	11	2	–	3	2	36
	8.8		*24.1*	*23.9*	*7.7*		*6.5*	*3.8*	*9.6*
Gopherus agassizii	4	5	–	–	1	5	–	1	16
	7.0	*8.3*			*3.9*	*16.1*		*1.9*	*4.3*
Crotaphytus wislizenii	1	1	–	2	3	1	–	–	8
	1.7	*1.7*		*4.4*	*11.5*	*3.2*			*2.1*
Sceloporus magister	–	–	2	–	–	–	–	–	2
			3.7						*0.5*
Dipsosaurus dorsalis	–	–	–	–	–	–	–	1	1
								1.9	*0.3*
Totals	57	60	54	46	26	31	46	53	373

noides was the most common species (33%), followed by *Cnemidophorus tigris* (28%), and *Uta stansburiana* (22%). *Phrynosoma platyrhinos* made up about 10% of the individuals found. The three other lizard species combined constituted less than 3% of the fauna; *Gopherus* was also a numerically minor part of the samples (4%).

There was considerable variation in the frequency of different lizards at different sites. At Barstow, about half of the lizards at site A was *Cnemidophorus*, whereas at site B about half was *Callisaurus*. *Uta* and *Phrynosoma* were most frequent at Stoddard Wells, and both sites in Anderson Valley had high proportions of *Cnemidophorus*, *Callisaurus*, and *Uta*. The Johnson Valley sites had exceptionally high numbers of *Callisaurus*.

Cnemidophorus was found in much larger numbers than *Callisaurus* at two sites (A, E) whereas the reverse was true at three sites (D, M, N), but the negative correlation between the numbers of these two species on the eight sites is not statistically significant (r_s = -0.50, $P >$ 0.05). These data suggest that these two species probably do not exclude one another.

Biomass

The large differences in total weights of reptiles between sites (Tables 1 and 3) were due largely to the uneven representation of the large-bodied tortoises. The tortoises alone constituted about 80% of the estimated biomass of the diurnal reptile community. The three commonest lizards made up only 16% of the total weight of the sampled fauna. The rank order of the contribution of each lizard species to the total biomass was as follows: *Cnemidophorus tigris*, *Callisaurus draconoides*, *Phrynosoma platyrhinos*, *Crotaphytus wislizenii*, and *Uta stansburiana*. Other lizards each contributed less than 1% (Table 3).

The distribution of lizard biomass was different from the proportion of individuals of each species. In both weight and numbers, *Callisaurus* and *Cnemidophorus* constituted the major segment of the lizard fauna (Tables 3 and 4). *Phrynosoma* and *Crotaphytus* were low in numbers, but when present they contributed appreciably to the total biomass. The numerically common *Uta* contributed a minor part of the total biomass because individual weights were only 2–3 g.

Discussion

I used the removal method on a total of 28 study sites: on 8 plots (16 ha) of undisturbed creosote-shrub habitat (present report), on 8 plots

Table 3. *Estimated biomass (in g per 2 ha) for tortoises and lizards at eight 2-ha sites. Mojave Desert, California. Percentage composition is in italics.*

	Barstow		Stoddard Wells		Anderson Valley		Johnson Valley		
Species	A	D	E	G	K	L	M	N	Total
Gopherus agassizii	2,545 *79.8*	3,860 *84.0*	–	–	1,000 *67.8*	8,675 *96.1*	–	500 *46.3*	16,580 *79.6*
Cnemidophorus tigris	353 *11.1*	369 *8.0*	219 *44.7*	162 *31.8*	237 *16.0*	175 *2.0*	159 *33.5*	139 *12.9*	1,813 *8.7*
Callisaurus draconoides	43 *1.4*	317 *6.9*	21 *4.3*	105 *20.6*	102 *6.9*	103 *1.2*	276 *58.2*	301 *27.9*	1,268 *6.1*
Phrynosoma platyrhinos	122 *3.8*	–	117 *23.9*	128 *25.2*	51 *3.4*	–	32 *6.8*	36 *3.3*	486 *2.3*
Crotaphytus wislizenii	75 *2.3*	28 *0.6*	–	62 *12.2*	76 *5.1*	39 *0.4*	–	–	280 *1.3*
Uta stansburiana	51 *1.6*	23 *0.5*	53 *10.8*	52 *10.2*	14 *1.0*	31 *0.3*	7 *1.5*	23 *2.1*	254 *1.2*
Dipsosaurus dorsalis	–	–	–	–	–	–	–	81 *7.5*	81 *0.4*
Sceloporus magister	–	–	80 *16.3*	–	–	–	–	–	80 *0.4*
Totals	3,189	4,597	490	509	1,480	9,023	474	1,080	20,842

(16 ha) of nearby disturbed land (Bury et al. 1977), and on 12 plots (24 ha) of sand dune habitat, half of which was damaged by off-road vehicles (R. B. Bury, unpublished data). I have also modified the method for censusing tortoise populations on two 25-ha plots in the Mojave Desert (Bury and Luckenbach 1977).

Most knowledge on desert reptiles has been obtained by intensive work at one or a few study areas, the approach typical of most research on desert reptiles; however, better comparative data may be available by extensive sampling at many sites. I suggest that the removal sampling technique is a promising tool for use in extensive surveys and population studies because it is an effective system to assess diurnal reptile communities.

Collecting efforts were most efficient (animals/hour effort) on the first day and somewhat less on the second day (Fig. 1). Few were found on subsequent searches. I suggest that a 2-day period (3 h/site per day) be used because collecting was still efficient on Day 2 and the second day appreciably increased the sample sizes (Figs. 1 and 2). Continued sampling apparently does not contribute enough additional information to justify the extra effort. Also, there are increased chances of emigration into the plots with longer sampling periods.

Workers may also want to try a thorough 1-day search (4 h in the morning, 2 h in the late afternoon or evening) or a 2-day regime of 4 h each day. Where animals may be shot, I believe that one collector can effectively search 2 or per-

Table 4. *Percentage composition of biomass of the lizard fauna taken on 2 days at eight 2-ha sites. Mojave Desert, California.*

	Barstow		Stoddard Wells		Anderson Valley		Johnson Valley		
Species	A	D	E	G	K	L	M	N	Total
Cnemidophorus tigris	54.8	50.1	44.7	31.8	49.4	50.3	33.5	24.0	42.5
Callisaurus draconoides	6.7	43.0	4.3	20.6	21.3	29.6	58.2	51.9	29.7
Phrynosoma platyrhinos	18.9	–	23.9	25.2	10.6	–	6.8	6.2	11.4
Crotaphytus wislizenii	11.7	3.8	–	12.2	15.8	11.2	–	–	6.6
Uta stansburiana	7.9	3.1	10.8	10.2	2.9	8.9	1.5	3.9	6.0
Sceloporus magister	–	–	16.3	–	–	–	–	–	1.9
Dipsosaurus dorsalis	–	–	–	–	–	–	–	14.0	1.9

haps 3 ha of creosote habitat in a 4-h period. Catchability of reptiles and local variables may alter the technique's effectiveness. For example, I found that two collectors can more efficiently locate fringe-toed lizards (*Uma*) than a single worker.

Pianka (1967) reported that four species of lizards are ubiquitous throughout the deserts of the western United States: *Cnemidophorous tigris*, *Uta stansburiana*, *Crotaphytus wislizenii*, and *Phrynosoma platyrhinos*. Eight other species are variously added in the southern parts of these deserts but more than 10 diurnal species are not known in any area. In the Mojave Desert, Pianka estimated that seven to nine species of flatland lizards were present. If I assume that *Xantusia vigilis*, a crepuscular species, and *Coleonyx variegatus*, a nocturnal form, were present on my study sites, the number of species in the creosote–shrub areas closely corresponds with Pianka's (1967) estimates.

The creosote–shrub community in the Mojave Desert is typified by five lizards (*Callisaurus draconoides*, *Cnemidophorus tigris*, *Uta stansburiana*, *Phrynosoma platyrhinos*, and *Crotaphytus wislizenii*) and the desert tortoise (*Gopherus agassizii*). Species diversity measures would be increased by the inclusion of nocturnal reptiles or species inhabiting other habitats such as sandy soils (*Dipsosaurus dorsalis*, *Uma* sp.) and rocky terrain (*Sauromalus obesus*, *Crotaphytus collaris*, *Sceloporus magister*). *Sceloporus magister* also occurs in a wide range of conditions and frequents areas with trees or tall shrubs in the Mojave Desert. *Urosaurus graciosus* is a shrub dweller in some areas of creosote. These assemblages may be found together where their habitats come into contact or interdigitate, and as many as 12 species of diurnal reptiles may be recorded in one area. For example, I have seen 10 of these 12 species at the Pisgah Crater, San Bernardino County, California. This area is a low lava flow with rocky habitat for *Sauromalus*, pockets of sand for *Uma* and *Dipsosaurus*, and adjacent creosotebush habitat where *Urosaurus* is common. Only *Crotaphytus collaris* and *Sceloporus magister* were not seen, but they may occur in the area.

In the present study, the reptiles species which were numerically most abundant did not constitute the largest component of the biomass. Thus, the energetic importance of each species would have been misunderstood if the weight data had not been analyzed. Among the lizards, three species (*Cnemidophorous*, *Callisaurus*, and *Uta*) were present on all sites. All are insectivorous but differ in body size and feeding strategies (Tinkle 1967; Pianka 1970; Parker 1972; Tanner and Krogh 1975). The other lizards are different in size and food habits: *Phrynosoma platyrhinos* is a medium-sized specialist on ants; *Crotaphytus wislizenii* is a large-bodied predator on lizards and large insects; *Sceloporus magister* is a heavy-bodied insectivore; and *Dipsosaurus dorsalis* is a large-sized herbivore. All seven of these lizards are morphologically distinct and belong to different genera. Each species plays a characteristic ecological role which overlaps little with other species. The importance of each species in the community can be better assessed by using information about biomass and habits in addition to numbers of individuals.

My data show that the desert tortoise (*Gopherus agassizii*) is a major component of the creosote–shrub community in the Mojave Desert. Due to its large size and local relative abundance, *Gopherus* contributes a significant proportion of the biomass and energy turnover in this ecosystem. It is an important herbivore in these arid-land habitats.

A transect 1.6 km long and about 7–8 m wide was employed by Pianka (1965) to assess lizard populations. This sampling area traverses a diversity of microhabitats as soil, topography, vegetation, and other factors change with distance. For example, a linear transect in most bajadas will include sandy soils in washes, whereas interfluvial areas are composed of grus, rocky soil, or desert pavement. Upper reaches of bajadas are usually rocky, grading through gravelly conditions into alkaline flats at lower elevations. Thus, transects across or down a bajada may display different diurnal reptile communities.

Site-specific studies such as those of Turner et al. (1969*a*, 1969*b*, 1970) provide valuable populational data on desert lizards, as intended, yet are generally inadequate to determine changes among several communities without an investment of great time. The removal method appears to be a useful compromise between these two approaches. The method encompasses a discrete plot of workable size (2 ha or more) in a relatively short time. Reptiles present can be related to different habitat variables such as vegetative structure and soils, which are needed to better elucidate the niche requirements of arid-land reptiles under various environmental regimes.

Much remains to be learned about the structure, variation, and composition of reptile communities in arid lands. Future studies should question the relations between species diversity, abundance, and biomass, and how these population features relate to habitat conditions. Generally acceptable and standardized techniques would enable valid comparisons of data collected by different workers and predictions of the effects of perturbations on these ecosystems.

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TROPICAL HERPETOFAUNA

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The Herpetofauna of Forest Litter Plots from Cameroon, Africa

by

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Abstract

Systematic samples of African forest litter herpetofaunas were made in Cameroon, Africa. Total species and taxonomic composition are compared between the African faunas and faunas from similar tropical forests of Asia and Central America. Data compared include total species and the taxonomic makeup of the samples.

Of special interest are the African samples that were taken in a forest established on a white-sand soil. This type of system is generally considered to be less productive than tropical forests growing on other types of soils, in Cameroon, the number of species was less than in Borneo or Costa Rica, but the number of individuals was about half of that found in Costa Rica and about six times that of Borneo.

In November-December 1975, the first quantitative herpetological collections from African wet forests, including systematic censuses of forest litter plots, were made in southwestern Cameroon, West Africa. This report compares these samples with similar studies in Borneo, Costa Rica, and Panama (Scott 1976).

The majority of the African samples was taken from a forest representing a well-defined subset of wet tropical forests – those growing on white-sand soils. These soils are found in many areas including parts of Borneo, Java, Malaya, Guyana, Suriname, Brazil, the Congo basin, and others. Janzen (1974) reviewed the known ecology of white-sand forests and hypothesized that they have a distinctive set of characteristics, chief of which are low fertility, relatively few tree species, well-protected tree leaves with an evergreen habit, slow recovery from disturbance, and low animal densities. The collections reported here enable us to test the latter generality.

Description of the Area

Collections were made at two sites in the Douala-Edéa Game Reserve which lies south of the Sanaga River near its mouth (Fig. 1). The first site was near a field station on the eastern shore of Lac Tissongo and the second at Lombé, a field camp about 5 km southwest of the southern tip of the same lake. The whole area is lowland, probably not more than 30 m elevation. McKey et al. (1978) described the soils and details of the biochemistry of the trees.

The terrain at the Lac Tissongo site consists of a low hill that slopes gently down to the lake shore. The litter samples were taken on flat sites on the hill. The soil is a loamy sand with excellent drainage. The evergreen forest is largely undisturbed except by trappers and hunters. It is rather low in stature (emergents to 40 m) compared with Costa Rican forests receiving an equivalent amount of rainfall, and lianas and epiphytes are less abundant. Collecting was done within 2 km of the station.

The Lombé site is a flat plain shallowly dissected with small streams. Swampy areas are common, and even on higher ground shallow puddles persist after a heavy rain. The soil is sand with little or no clay and appears to conform well to the tropical white-sand forests de-

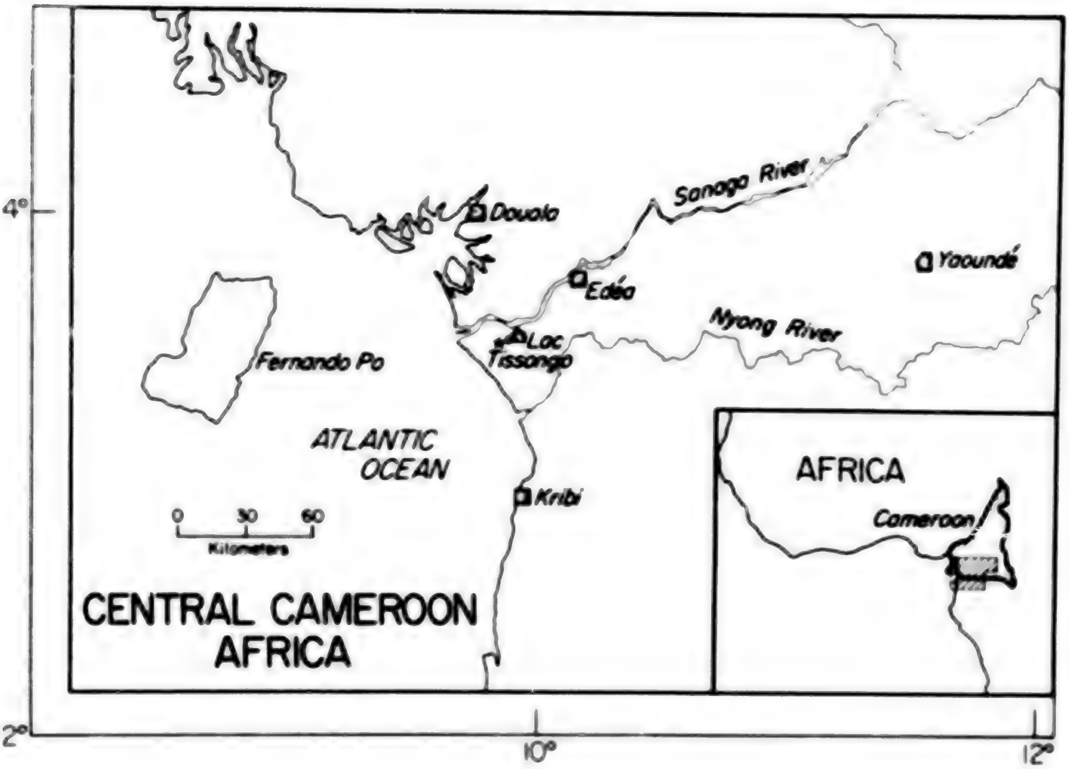

Fig. 1. Central Cameroon, Africa, showing location of study sites. The triangle is the Lac Tissongo camp; the star is Lombe.

scribed by Janzen (1974). The forest is well developed and only slightly shorter than at Lac Tissongo, but lianas are even rarer. There is only one palm; understory species are scarce. The litter samples were taken from a well-drained upland site, and all collections were made within 2 km of camp.

Rainfall in the two areas is about 4 m annually; an average of about 3 months receives less than 100 mm of rain (Suchel 1972). The samples were taken during the early part of the dry season.

Litter depth, measured at five points in each plot, averaged 2.6 cm at Lac Tissongo and 1.8 cm at Lombe. The litter was similar in depth and structure to that in Costa Rican lowland forests except that it was tightly bound together by fungal hyphae. Litter was thicker in the area of windfalls and under the emergent tree *Lophira*, which is one of the few synchronously deciduous trees in the forest (D. McKey, personal communication).

The forests on the two sites contain relatively few tree species in comparison with tropical forests on more fertile soils (D. McKey, personal communication). Mammals were moderately common and included several species of monkeys and prosimians, chimpanzees, pangolins, bush pigs, seve[illegible]ets, mongooses, porcupines, watert[illegible] species of duikers, tree hyraxes, and e[illegible]

Methods

During late November and early December 1975, 15 square 58-m² plots were randomly located on the forest floor and cleared of litter. Five were at Lac Tissongo and 10 at Lombe. All frogs seen were tabulated and captured if possible. For further details of the methods used, see Lloyd et al. (1968) and Scott (1976). The results of these samples are compared with similar samples reported from La Selva and Osa, Costa Rica (Scott 1976); Sarawak, Borneo (Lloyd et al. 1968); and Barro Colorado Island, Panama (Heatwole and Sexton 1966; Myers and Rand 1969).

General collections were made in April (4 days, early wet season), November (18 days), and December (6 days, early dry season) 1975. A variety of techniques were employed during a total of about 66 man-hours. These collections serve as the basis for estimating the total number of species present. Two species, a cobra (*Naja*) and a monitor (*Varanus*), were seen and tabulated but not collected.

Results and Discussion

Comparison between Lac Tissongo and Lombe

Little difference existed between the two sets of African litter plots, especially in species composition (Table 1). The Lac Tissongo samples yielded fewer animals per plot ($\bar{x} = 3.8$) than the Lombe plots ($\bar{x} = 6.3$). The difference was not statistically significant (Mann-Whitney U test: $P > 0.10$), but Lac Tissongo may have lower densities. The samples are small, and half of the total Lombe plots each produced more animals than any one of the Lac Tissongo samples. The difference in the number of animals may be a result of topography. In Costa Rica slope samples regularly contained fewer animals (Scott 1976), probably because of the drier and more seasonal conditions on the well-drained upland soils. The Tissongo samples were taken in hilly terrain whereas the Lombe plots were in flatland forest.

The data from the two African sites are lumped for the regional comparisons that follow. Table 2 is a list of 38 species collected from the African sites. I have indicated those that I consider to be regular litter inhabitants.

Animal Densities

The African litter plots are compared with samples taken from other lowland tropical areas with similar climates and vegetations (Table 3). Animal densities are 55-65% of those found in the lowlands of Costa Rica and Panama and six times the densities in Borneo. There were no lizards or snakes in the African plot samples.

African frog densities are surprisingly high considering the fact that two-thirds of the samples were taken from a white-sand forest. Theoretically, these forests are growing in a nutrient-poor environment that severely limits tree growth rates and other primary production (Janzen 1974). Therefore the trees hold individual leaves much longer and protect them with toxins and digestion-reducing compounds (McKey et al. 1978). When the leaves fall, they decompose very slowly because of the presence of these substances. To the litter community dependent on leaf fall for the great majority of its energy, this means that fewer leaves are decomposed and nutrients are released slowly. The Lombe forest had many of the characteristics of the white-sand system (McKey et al. 1978): white-sand subsoil; clear blackwater lakes and rivers (presumably from dissolved humic acids); a lack of synchronous or heavy leaf fall (except for *Lophira*); very few epiphytes and lianas; few mosquitoes; stunted crops; sparse second growth; few tree species; and low understory insect densities (D. McKey, personal communication). On the other hand, the streams contained a moderate number of fish, and mammals and birds were reasonably common in the forest. Evidently Lombe does not represent as extreme development of the white-sand forest as was studied by Janzen and Inger in Borneo (Janzen 1974). Possibly the African litter frogs have adopted certain of the adaptive strategies used by the trees. If that were true, we would expect them to be long-lived, unusually toxic, and to produce few young. Thus, the standing crop

Table 1. *Occurrence of frogs in 15 Cameroonian forest litter plots. Samples taken in November and December 1975*

Species	Lac Tissongo (5 plots)	Lombe (10 plots)	Totals (15 plots)
Bufonidae			
Nectophryne batesi	1		1
N. afra	3	3	6
Bufo gracilipes	1		1
Ranidae			
Arthroleptis adelphus	6	22	28
A. sylvaticus	6	24	30
A. variabilis		3	3
Hylarana albolabris	1	4	5
Phrynobatrachus cornutus		4	4
Escaped frogs	1	3	4
Totals	19	63	82
Individuals/100 m²	6.5	20.8	9.4
Number of Species	6	6	8

Table 2. *Reptiles and amphibians collected and observed near Lac Tissongo, Cameroon, Africa.*

Species	Litter species	Lac Tissongo camp	Lombé
Amphibia			
Bufonidae			
Bufo camerunensis	X	X	–
B. gracilipes	X	X	X
Nectophryne afra	X	X	X
N. batesi	X	X	X
Ranidae			
Hylarana albolabris	X	X	X
H. sp. nov.		–	X
Phrynobatrachus auritus	X	X	X
P. cornutus	X	–	X
Ptychadena aequiplicata	X	–	X
Petropedetes newtoni	X	–	X
Conraua crassipes	–	–	X
Arthroleptis adelphus	X	X	X
A. sylvaticus	X	X	X
A. taeniatus	X	–	X
A. variabilis	X	X	X
Hyperoliidae			
Leptopelis aubryi		X	–
L. brevirostris	–	X	X
L. boulengeri	–	–	X
L. millsoni	–	–	X
Reptilia			
Lacertilia			
Gekkonidae			
Hemidactylus echinus		X	X
H. fasciatus		X	X
H. muriceus	X	X	X
Lygodactylus conraui	–	–	X
L. fischeri	–		X
Scincidae			
Mabuya affinis	X	X	X
M. polytropis	X	–	X
Panaspis breviceps	X	–	X
P. reichenowi	–	X	–
Chamaeleontidae			
Chamaeleo cristatus	–	X	–
C. quilensis	–	X	X
Lacertidae			
Holaspis guentheri	–	–	X
Varanidae			
Varanus sp.	X	–	X
Serpentes[a]			
Boidae			
Python sebae		–	X
Elapidae			
Naja sp.		–	X
Colubridae			
Boiga pulverulenta		–	X
Dipsadoboa unicolor		–	X
Philothamnus semivariegatus		–	X
Thelotornis kirtlandi		X	

[a]Snakes were not considered to be part of the litter herpetofauna

would be relatively high but population turnover may be reduced compared with areas containing more soil nutrients.

The lack of lizards and snakes in the African litter samples reflects a real difference between them and the forests studied in Borneo and Central America. The only analog of stem-perching litter-feeding lizards of the American genera *Anolis* and *Norops* was a scarce diurnal gecko, *Hemidactylus muriceus*, and *Panaspis breviceps* was the only African lizard similar to the American litter microteids or the diurnal gecko, *Lepidoblepharis*. Mongooses (*Herpestes auropunctates*) were seen several times during the study, and perhaps Janzen's (1976) hypothesis that African reptile faunas are suppressed by small omnivorous predators applies here.

The only common terrestrial lizards were quick, heliothermic skinks, ecologically similar to New World *Ameiva*. They were found near houses or in windfall clearings that contained tangles of dead and living vegetation. Arboreal lizards were somewhat more common and widespread. Adult *Varanus* were seen twice. They are probably semi-aquatic and resistant to mongoose predation.

During 66 collecting hours in Cameroon, I took a *Thelotornis* and a *Python* and saw a *Naja*. Three other snakes were brought to me: a *Boiga*, a *Dipsadoboa*, and a *Philothamnus*. Herpetologists on Barro Colorado Island, Panama, took 11 species during 91 h of wet-season

Table 3. *Comparison of litter plot samples from American, Asian, and African tropical lowlands. Bornean data from Lloyd et al. (1968), Costa Rican from Scott (1976), and Panamanian from Heatwole and Sexton (1966) and Myers and Rand (1969).*

Region	Area within plots (m^2)	Individuals per 100 m^2	No. of species taken in litter plots	No. of regular litter species
Sarawak (Borneo)	23,342	1.5	41	38
La Selva and Osa (Costa Rica)	2,266	17.1	23, 23	34, 35
Barro Colorado Island (Panama)	512	14.6	15	27
Lac Tissongo and Lombé (Cameroon)	872	9.4	8	~18

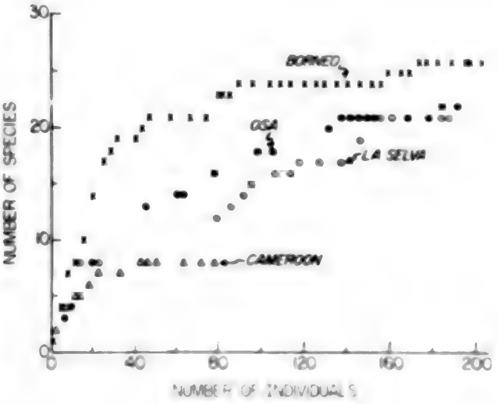

Fig. 2. Number of species collected in first 78 or more specimens of litter plot reptiles and amphibians in Cameroon; La Selva and Osa, Costa Rica (Scott 1976); and Borneo (Lloyd et al. 1968).

collecting, and 6 species during 54 h in the dry season (Myers and Rand 1969). In Costa Rica, collectors usually take at least one to three snakes per day in lowland wet forest. All of the Cameroonian snakes I collected were arboreal or well protected by venom or size, even though mongooses can probably take them under some circumstances (Struhsaker and McKey 1975). These observations of relatively low snake densities and the species composition of my Cameroonian collections are similar to Janzen's (1976) reptile census data and support his suggestion that predation is an important regulator of African reptile population densities.

Species Number

The number of species in the African litter samples is only about half of that found in equivalent-sized samples from the other tropical areas (Table 3). Curves plotting the number of species vs. the number of individuals in the different tropics show a steady rise to 17 to 21 species in Borneo and Central America, whereas the African samples plateau at 8 species (Fig. 2). If a plateau is considered to be the collection of 20 or more specimens without adding a new species, the first La Selva, Borneo, and Osa plateaus represent respectively 50, 55, and 60% of the total number of litter species. If eight species represent 55% of the African fauna, we would expect 15 regular litter species. This is somewhat low since I have tabulated 18 (Table 2), but our knowledge of the habits of the African species is scanty, and some of the "litter" species may not belong in that category.

A depression in the number of species of frogs and lizards in a Bornean white-sand forest has been reported by Inger (*in* Janzen 1974). A white-sand site had 37 species (litter and non-litter species) whereas two non-sand forests yielded 66 and 84 species, respectively. Janzen interpreted this to mean that the white-sand forest was a relatively harsh environment that was inhabited by a small number of well-adapted species.

The African general collections yielded about the same proportion of lizard species (32%) as appear in Costa Rican litter faunas (26% La Selva, 31% Osa). In Borneo, 45% of the fauna was lizards. Heyer and Berven (1973) and Scott (1976) suggest that the American frog genus *Eleutherodactylus* serves as an ecological replacement for small lizards because of its capability to undergo development independently of free water. In Cameroon, the genus *Arthroleptis* has a similar capability and were the commonest frogs in the litter samples.

Although the African litter samples yielded relatively few species, the total forest habitat seems to hold a substantial number. Comparison of the number of species vs. collecting hours for Cameroon and Barro Colorado Island, Panama, shows very similar curves (Fig. 3). Duellman and Myers collected 43 species of reptiles and amphibians in 91 man-hours on Barro Colorado Island in the wet season (Myers and Rand 1969), and I took or saw 35 species in 66 h. Barro Colorado Island contains about 100 species of reptiles and amphibians. It is very likely that Lombé and Lac Tissongo harbor nearly as many, since no frogs were breeding during the collecting periods, and frog choruses are favorite sources of diverse samples for herpetologists.

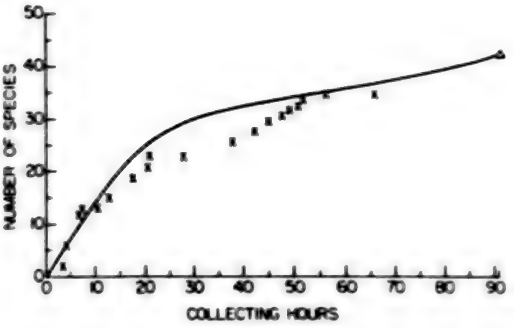

Fig. 3. Cumulative number of reptile and amphibian species collected per collecting hour in Cameroon (X) and Panama (curve and △; Myers and Rand 1969).

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SANDY SOIL HERPETOFAUNAS

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Herpetofaunal Survey of the Sinai Peninsula (1967–77). with Emphasis on the Saharan Sand Community[1]

by

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Abstract

The local interest in biogeography and ecology, and the paucity of data from areas surrounding Israel, led to intensive herpetological collecting in Sinai in 1956–57 and since 1967. Material in the Hebrew University of Jerusalem and in Tel-Aviv University together exceeds 1,000 specimens, comprising one species of toad, *Bufo viridis*, four species of marine turtles, and 50 species of terrestrial reptiles. Of these, one was first reported from Sinai in 1957, nine in 1973, and two, *Caretta caretta* and *Rhynchocalamus melanocephalus*, herein. Twenty-two species which occur in contiguous areas of Israel or Egypt or both, or have been reported from Sinai in the literature, were absent in the collected material. The sand dunes of northern Sinai are inhabited by a "community" of 10 psammophile reptile species of Saharan or Saharo–Arabian distribution. Each represents a different family or a genus of distinctive body size. Resource partitioning between related forms is sometimes indicated. Several other species which are not strict psammophiles (mainly snakes) also occur in these dunes.

The land bordering the eastern Mediterranean Sea is of great ecological-biogeographical interest (Furth 1975). Wallace's (1876) concept of a vast circum-mediterranean Mediterranean Region of heterogeneous or transitional nature is no longer acceptable to local biogeographers. Instead, four major ecological-biogeographic regions are now distinguished in the area (Bodenheimer 1956; Zohary 1970, 1973), and this division appears applicable to the herpetofauna (Bodenheimer 1937; Werner 1971). These regions are the Mediterranean (*sensu stricto*) scrubland and woodland (annual precipitation usually above 300 mm), the Saharo-Arabian desert (annual precipitation usually much under 150 mm), the intervening Irano-Turanian steppe (intermediate and irregular rainfall), and the hot and dry Sudanian (Ethiopian) penetration area (Haas and Werner 1969:367–368, Fig 13; Zohary 1970:map c).

In Israel the Irano-Turanian is only a narrow belt between the Mediterranean in the North and the desert in the South. Consequently there is an abrupt transition (or very steep gradient) between the two floristic regions. The fauna of the Irano-Turanian is poorly developed so that the sudden break between desert and non-desert enhances the interest of various ecological problems to local biologists.

However, before 1967 Israeli herpetologists were restricted to studying reptiles and their distributions within confined and unnatural spatial boundaries. These boundaries could not be transcended nor could much information be obtained regarding reptile populations in adjacent areas. Thus, when access to the Sinai peninsula was gained, briefly in the winter of 1956–57 and again since the summer of 1967, Israeli herpetologists (in common with other scientists) endeavored to research the area thoroughly.

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[1] Dedicated to the memory of Hermann Zinner, who lived to see but the budding fruit of his love for desert reptiles.

[2] This report was prepared while the author was a visiting associate professor at the Department of Anatomy, University of Chicago, Chicago, Illinois.

The landscapes of the Sinai Peninsula consist of sand dunes in the north, hills of sedimentary limestone and alluvial flats in the center, and steep mountains of ancient sandstone and magmatic rocks in the south. Biogeographically, the northern and central parts are Saharo-Arabian, the southern high mountains (above 1,500 m) are Irano-Turanian, and the southeastern and southwestern slopes of these mountains are Sudanian (Bodenheimer 1937; Zohary 1970; Haim and Tchernov 1974).

Previously the herpetofauna of Sinai was poorly known because collecting in the area had always been difficult, especially in terms of administration, logistics, and personal safety. The main relevant publications are those by Heyden (1827), Hart (1891), Barbour (1914), Bodenheimer (1937), Haas (1943), Schmidt and Marx (1956), and Hoofien (1965); some attention has also been given to Sinai in works on the Egyptian herpetofauna by Anderson (1898), Flower (1933), Loveridge (1947), and Marx (1968). Marx (1968) reported on material mainly from two circumscribed areas in Sinai, the El 'Arish area in the northern dunes and the Gebel Katherina range in the southern mountains. Two of these contributions contain formal checklists of the herpetofauna of Sinai: Flower (1933:738–740) who comments (p. 737), "Sinai is the richest part of Egypt herpetologically; it is by no means completely explored, and yet 42 species are known," and Schmidt and Marx (1956:37) who list 50 discrete taxa.

Some results of the recent extensive collecting were summarized by Hoofien (1972), Werner (1973), and Zinner (1974). An updated reptile checklist for Israel and Sinai is currently being compiled (Hoofien and Werner, unpublished data), employing manually prepared locality-record maps (Werner 1977). Moreover, for the more common squamate species, a detailed computerized study of geographical variation of meristic and mensural characters (for the area Turkey–Sinai, inclusive) is under way (Kosswig et al. 1976, Kosswig and Werner, unpublished data). The purpose of the present paper is (1) to give a brief interim report of the herpetological survey of Sinai, indicating the material and the main results, in terms of species found and species expected but not found, and (2) to point out certain noteworthy aspects of the herpetofaunal component of the Saharan sand dune community of northern Sinai. Reference is made only to the principal papers dealing with the distribution and identification of the various species. It is impossible to review here the literature on the biology and ecological physiology of the species, although the literature is mostly based on adjacent Egyptian or Negev populations and hence relevant.

Materials and Methods

This report relies on the herpetological material from Sinai in the zoological museums of the Hebrew University of Jerusalem (HUJ; over 700 specimens) and of Tel-Aviv University (TAU; over 300 specimens). It has been impractical to examine the material which may be available in minor collections throughout Israel. Much of the material used had been collected in the course of a survey of the distribution of rodents throughout Sinai (Haim 1969). Other material had been added by numerous travelers, often on field trips with extraneous objectives, or incidentally to service in the Army. Most of these trips followed popular routes to selected localities. Very few trips (essentially, mine) were specially planned to collect reptiles along transects from which data were lacking.

Specimens in the collections were identified by standard keys (Barash and Hoofien 1956; Marx 1968) or more specific literature when necessary. The material was listed on species sheets with the locality data, which were then entered on species maps by topographical grid references (Werner 1977). Where original locality records lacked grid references, the latter were reconstructed from Survey of Israel, Ministry of Labour, maps or consultation with the collectors.

Locality record maps for 48 species were presented elsewhere (Werner 1973) and are not repeated here, although some additional records have been obtained. Perusal of these maps shows a general lack of data from two areas: the alluvial flats (around Qal'at en Nakhal) in central Sinai, an uninteresting landscape largely shunned by field trips, and the Suez Canal area where travel commonly was risky or forbidden.

Taxonomic names used in this report are those currently accepted by Israeli herpetologists (Hoofien 1972; Werner 1973).

Results and Comments

Species Found

Of the species known to inhabit the Sinai (Table 1), the only amphibian represented is *Bufo viridis* and that only from the northeast corner of Sinai. Here, as in the Negev of Israel, this Palearctic toad reaches the southern (desertic) limit of its distribution (Werner 1948; Wahrman 1970). Specific searches and inquiries for other frogs, especially in the larger oases, remained fruitless.

Of the Chelonia, *Testudo kleinmanni* occurs in the northern dunes, and *Caretta caretta*, *Chelonia mydas*, *Eretmochelys imbricata*, and *Dermochelys coriacea* are represented from the Sinaitic Mediterranean and Red Sea shores.

Of the Sauria, the Gekkonidae are represented by eight or nine species: *Cyrtodactylus scaber*, *Hemidactylus flaviviridis*, *H. turcicus turcicus*, *Ptyodactylus hasselquistii guttatus*, *P. h.* cf. *hasselquistii*, *Stenodactylus petrii*, *S. sthenodactylus sthenodactylus*, *Tarentola mauritanica mauritanica*, and *Tropiocolotes steudneri*. The two *Ptyodactylus* forms, currently regarded as subspecies (Werner 1965), may well be distinct species. *P. h. guttatus* occurs in northern Sinai and in the south on mountains, whereas *P. h.* cf. *hasselquistii* lives inside the wadis and canyons of the south. The two are sympatric in the Abu Zanima area on the Gulf of Suez and their vocalizations differ markedly (Frankenberg 1974; Werner et al. 1978). By studying the diel activity cycle in an aktograph, Frankenberg (1976, 1977, 1978, 1979) found that *P. h. hasselquistii* is more nocturnal than *P. h. guttatus*. The taxonomy of the group is presently under review (Y. L. Werner, unpublished data).

Agamidae.—Six species: *Agama pallida pallida*, *A. savignii*, *A. sinaita*, *A. stellio brachydactyla*, *A. stellio* subsp., *Uromastyx aegyptius* and *U. ornatus*. The nomenclature for *Agama pallida* has been discussed elsewhere (Werner 1971:228). Despite the work of Daan (1967), the taxonomy of *Agama stellio* in Sinai remains uncertain. *A. s. brachydactyla* occurs in the north but southern specimens are different, as has also been suggested by Flower (1933:775).

Chamaeleonidae.—Specimens available from the northern dunes are juveniles, apparently assignable to *Chamaeleo chamaeleon musae*; some may be intergrades between *C. c. musae* and *C. c. recticrista* Boettger, 1880, of Mediterranean Israel (Hoofien 1964).

Scincidae.—Five species: *Ablepharus kitaibelii*, *Chalcides ocellatus*, *Eumeces schneideri schneideri*, *Scincus scincus*, and *Sphenops sepsoides*. Part of the distribution of *Sphenops sepsoides* was presented earlier (Werner 1968) on the basis of the 1956–57 Sinai expeditions.

Lacertidae.—Six species: *Acanthodactylus boskianus asper*, *A. scutellatus scutellatus*, *Eremias brevirostris*, *E. guttulata*, *E. olivieri*, and *E. rubropunctata*. Some authors (e.g., Marx 1956, 1968) do not distinguish between *Eremias guttulata* and *olivieri* but they are indeed distinct in morphology (Haas 1951*a*; Barash and Hoofien 1956) and habitat: *guttulata* occurs on various soils including rocks but not on sand; *olivieri* occurs on sand and sand mixtures; in some places the two occur together but suspected hybrids are rare. The occurrence of *Eremias brevirostris* in southernmost Sinai was first reported by Hoofien (1957) on the basis of specimens from the 1956–57 expeditions.

Varanidae.—There is only one specimen, *Varanus griseus griseus* (TAU), probably because the species is both protected and difficult to capture.

Among the Ophidia, the Typhlopidae are represented by *Typhlops vermicularis* and the Leptotyphlopidae by *Leptotyphlops macrorhynchus* (= *L. phillipsi* Barbour 1914; Hahn 1978), the occurrence of which has recently been reconfirmed in the Santa Catherina area.

Colubridae.—Eight "aglyphous" species: *Coluber jugularis asianus*, a single specimen from Gebel Hillal in northeastern Sinai (TAU), the species-group has recently been revised by H. Zinner in an unpublished dissertation; *C. ravergieri nummifer* (from Wadi Feiran only), *C. r. rhodorhachis*, *C. rogersi*, *Eirenis coronelloides*, *Lytorhynchus diadema*, *Rhynchocalamus melanocephalus*, and *Spalerosophis diadema cliffordi*.

Five "opisthoglyphous" species: *Malpolon moilensis*, *Psammophis aegyptius*, *P. schokari*, *Telescopus dhara*, and *T. hoogstraali*. According to Zinner (1977) *T. hoogstraali* is a subspecies of *T. fallax* (Fleischmann, 1831).

Elapidae.—Only *Walterinnesia aegyptia*.

Viperidae.—Five species, *sensu lato*: *Atractaspis engaddensis*, *Cerastes cerastes*, both horned and unhorned specimens; *C. vipera*; *Echis colorata*, and *Pseudocerastes fieldi*. Sochurek (1974) has claimed priority for a new subspecies,

Table 1. *Amphibian and reptile species from the Sinai. One asterisk indicates species first reported by Werner (1973); two asterisks indicate those found since then; three asterisks indicate species probably present but never recorded.*

- AMPHIBIA
  - Salientia
    - Bufonidae
      - *Bufo viridis* Laurentius, 1768
- REPTILIA
  - Chelonia
    - Testudinidae
      - *Testudo kleinmanni* Lortet, 1883
    - Cheloniidae
      - *Caretta caretta* (Linnaeus, 1758)**
      - *Chelonia mydas* (Linnaeus, 1758)*
      - *Eretmochelys imbricata* (Linnaeus, 1758)*
      - *Dermochelys coriacea* (Linnaeus, 1766)*
  - Sauria
    - Gekkonidae
      - *Cyrtodactylus scaber* (von Heyden, 1827)
      - *Hemidactylus flaviviridis* Rueppell, 1835
      - *H. turcicus turcicus* (Linnaeus, 1758)
      - *Ptyodactylus hasselquistii guttatus* von Heyden, 1827
      - *P. h.* cf. *hasselquistii* (Donndorff, 1798)
      - *Stenodactylus petrii* Anderson, 1896
      - *S. sthenodactylus sthenodactylus* (Lichtenstein, 1823)
      - *Tarentola mauritanica mauritanica* (Linnaeus, 1758)
      - *Tropiocolotes steudneri* (Peters, 1869)
    - Agamidae
      - *Agama pallida pallida* Reuss, 1833
      - *A. savignii* Duméril and Bibron, 1837
      - *A. sinaita* von Heyden, 1827
      - *A. stellio brachydactyla* Haas, 1951*
      - *A. stellio* (Linnaeus, 1758) subspecies
      - *Uromastyx aegyptius* (Forskal, 1775)
      - *U. ornatus* von Heyden, 1827
    - Chamaeleonidae
      - *Chamaeleo chamaeleon musae* (Steindachner, 1900)
    - Scincidae
      - *Ablepharus kitaibelii* Bibron and Bory, 1833
      - *Chalcides ocellatus ocellatus* (Forskal, 1775)
      - *Eumeces schneideri schneideri* (Daudin, 1802)
      - *Scincus scincus* (Linnaeus, 1758)
      - *Sphenops sepsoides* (Audouin, 1829)
    - Lacertidae
      - *Acanthodactylus boskianus asper* (Audouin, 1829)
      - *A. scutellatus scutellatus* (Audouin, 1829)
      - *Eremias brevirostris* (Blanford, 1874)
      - *E. guttulata* (Lichtenstein, 1823)
      - *E. olivieri* (Audouin, 1829)*
      - *E. rubropunctata* (Lichtenstein, 1823)
    - Varanidae
      - *Varanus griseus griseus* (Daudin, 1803)
  - **Ophidia**
    - Typhlopidae
      - *Typhlops vermicularis* Merrem, 1820
    - Leptotyphlopidae
      - *Leptotyphlops macrorhynchus* (Jan, 1864)
    - Boidae
      - *Eryx jaculus* (Linnaeus, 1758)***
    - Colubridae
      - *Coluber jugularis asianus* Boettger, 1880*
      - *C. ravergieri nummifer* Reuss, 1834
      - *C. r. rhodorhachis* (Jan, 1865)
      - *C. rogersi* (Anderson, 1893)
      - *Eirenis coronelloides* (Jan, 1862)
      - *Lytorhynchus diadema* (Duméril and Bibron, 1854)
      - *Macroprotodon cucullatus* (Geoffroy St. Hilaire, 1827)***
      - *Malpolon moilensis* (Reuss, 1834)*
      - *M. monspessulanus* (Hermann, 1804)***
      - *Psammophis aegyptius* Marx, 1958*
      - *P. schokari* (Forskal, 1775)
      - *Rhynchocalamus melanocephalus* (Jan, 1862)**
      - *Spalerosophis diadema cliffordi* (Schlegel, 1837)
      - *Telescopus dhara* (Forskal, 1775)
      - *T. hoogstraali* Schmidt and Marx, 1956
    - Elapidae
      - *Walterinnesia aegyptia* Lataste, 1887*
    - Viperidae
      - *Atractaspis engaddensis* Haas, 1950
      - *Cerastes cerastes* (Linnaeus, 1758)
      - *C. vipera* (Linnaeus, 1758)
      - *Echis coloratus* Günther, 1878
      - *Pseudocerastes fieldi* Schmidt, 1930

Cerastes cerastes karlhartli (southwestern Sinai), without differentiating it from the typical form.

Comparison of this herpetofaunal list with lists of adjacent Israel (Cisjordan) (Haas 1951*b*, 1952; Werner 1966), Jordan (Transjordan) (Haas 1943, 1951*b*; Werner 1971), and Africa (Egypt) (Anderson 1898; Flower 1933; Marx 1968) shows that the herpetofauna of Sinai, as represented by the recent collections, is not exactly identical with any of the other areas (Fig. 1). On the other hand, none of the species is strictly endemic to Sinai, although *Uromastyx ornatus* extends only slightly into southern Israel.

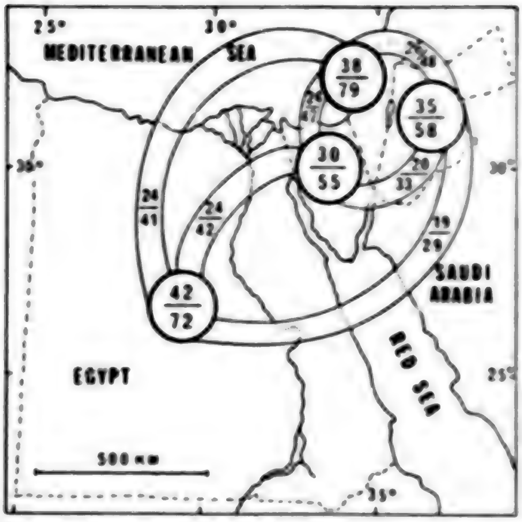

Fig. 1. Relations of the reptilian fauna of Sinai to those of surrounding Israel, Jordan, and Egypt. Broken lines demarcate survey areas; figures in circles represent the number of lizard species (numerator) and the total number of land and freshwater reptile species (denominator) in each. Figures in connecting arcs represent the numbers of species in the two categories that are common to two areas. The data for lizards are given because these are probably more complete than those for snakes, and to facilitate comparison with Anderson's (1968:367) similar diagram for southwestern Asia.

Species Not Found

Three species of snakes (*Eryx jaculus*, *Macroprotodon cucullatus*, and *Malpolon monspessulanus*) known from both southern Israel and Egypt are not represented in my material (nor reported in the literature) from the intervening Sinai but very probably occur in that area.

On the other hand, three reptiles (*Trionyx triunguis*, *Mabuya vittata*, and *Natrix tessellata*) known from both Israel and Egypt and not represented in the collections may actually be absent from Sinai due to the scarcity or absence of suitable habitats. *Natrix tessellata* occurs in Yemen as well but probably as a relict (Leviton 1977). Its single literature record from Sinai has been discussed by Hoofien (1965). Absence of suitable habitats may likewise apply to *Mabuya quinquetaeniata*, which occurs in Egypt as far east as the west bank of the Suez Canal, or the Suez Canal may act as a barrier for this and other species.

Several other reptiles not represented in my material have been reported at one time or another from Sinai in the literature (details in Flower 1933; Hoofien 1965; Marx 1968): *Pelomedusa subrufa* (apparently an error); *Hemidactylus sinaitus* (recent material from Sinai does not fully conform to the description); *Tarentola annularis* (no explanation suggested); *Tropiocolotes nattereri* (likely to be confirmed on reexamination of the material); *T. tripolitanus* (Marx's 1968 record was based on a half-dried specimen from El 'Arish [U.S. National Museum of Natural History no. 133490] which I identify as a juvenile *Stenodactylus petrii*); *Agama mutabilis* (the specimens on which this is based differ from North African ones and are assignable to *A. pallida*); *Uromastyx acanthinurus* (no explanation); *Acanthodactylus pardalis* (erroneously based on an *A. boskianus*, H. Marx, personal communication, a piquant situation since the species abounds in both Egypt and the Negev of Israel but its preferred loess soil does not occur in Sinai); *A. cantoris* (erroneous); *Eremias mucronata* (probably erroneous); *Latastia longicaudata* (either introduced or erroneous); *Ophisops elegans* (probably correct for restricted habitats); *Coluber sinai* (no explanation); *Eirenis coronella* (refers to *E. coronelloides*, J. H. Hoofien, personal communication). Additionally, a record of *Coluber elegantissimus* (Negumi 1949) awaits verification.

The total herpetofauna of Sinai may include at least 60 species.

The Saharan Psammophile Community

Of all the reptiles of Sinai, those inhabiting the northern sand dunes constitute the most clearly defined community, or community fraction, in that many of them are strict psammophiles not occurring on adjacent soils (Table 2). The morphological adaptations of such species to life in and on sand have been discussed by Buxton (1923), Mosauer (1932, 1936), and many others. In terms of ecological biogeography, the core of this community comprises 10 truly psammophilous species of essentially Saharan, or Saharo-Arabian, distribution. Together with many other psammophilous organisms, they support the characterization of these dunes, which are indicated on maps presented by Werner (1968) and Haim and Tchernov (1974), as an extension of the Sahara (*sensu lato*).

Table 2. *Amphibians and reptiles of the northern Sinai sand dunes.*

Psammophile Species
  Testudo kleinmanni
  Stenodactylus petrii
  Agama savignii
  Scincus scincus
  Sphenops sepsoides
  Acanthodactylus scutellatus
  Eremias olivieri
  Varanus griseus
  Lytorhynchus diadema
  Cerastes vipera
Euryoecious Species
  Stenodactylus sthenodactylus
  Coluber rogersi
  Spalerosophis diadema
  Psammophis schokari
  Walterinnesia aegyptia
Species of Particular Microhabitats
  Bufo viridis
  Hemidactylus turcicus
  Tarentola mauritanica
  Chamaeleo chamaeleon

Interestingly, each of the species represents a different family, or at least a genus of distinct body size; no two members of any one genus are included. In most instances, however, vicarious congeners occur on the adjacent non-sandy soils, and often other psammophilous congeners occur on disjunct sand areas elsewhere in Sinai or Israel. Thus the Testudinidae are represented in the Saharan north Sinai dunes by *Testudo kleinmanni*, which is replaced by *T. graeca* in the more northern coastal plain dunes (and other soils) of Israel. Among the Sauria, in the family Gekkonidae, *Stenodactylus petrii* is replaced in the Wadi Araba dunes by *S. doriae*, and on other light soils by *S. sthenodactylus*. This latter species also occurs in the dunes, especially north of the range of *S. petrii*, but also sympatrically with it (Haas 1956; Werner and Broza 1969). In the Agamidae, *Agama savignii* is replaced on adjoining loess soils, and on sands elsewhere, by *A. pallida*. The two skinks, *Scincus scincus* and *Sphenops sepsoides*, coexist. *Scincus scincus* is limited to these dunes, whereas *S. sepsoides* also occurs in sand elsewhere. Where the latter does not occur, *Chalcides ocellatus*, normally inhabiting other soils, occurs in the sand. I found these two species together only at the northern extreme of the range of *S. sepsoides*, near Caesarea on the Mediterranean coast. The lacertid, *Acanthodactylus scutellatus*, is replaced by *A. boskianus* on adjacent light soils and on unconnected Sinai sands, and by *A. schreiberi* on northern Israel's coastal dunes (Werner 1952); *Eremias olivieri* is replaced on adjacent non-sand by *E. guttulata*, although the two may coexist on sandy loess. *Varanus griseus* is the only varanid of the area. *Lytorhynchus diadema* is the only sand-limited colubrid in the area. *Cerastes vipera* is the sand viper of the northern dunes, and is replaced on inland sands by *C. cerastes* or *Pseudocerastes fieldi* and on other soils by *Echis colorata*. Excellent descriptions and illustrations of almost all of these species were provided by Anderson (1898).

Population density has not been estimated for any of the species. From observations and collecting, *Acanthodactylus scutellatus* is by far the most common cursorial diurnal reptile on the dunes, although its density may well be matched by that of the subterranean *Sphenops sepsoides*, and perhaps by the nocturnal *Stenodactylus petrii*. *Eremias olivieri* and *Scincus scincus* appear to be much rarer.

In some instances there are indications of how competition between related forms may be reduced. Of the two sympatric *Stenodactylus* species, *petrii* has much larger eyes than *sthenodactylus*, implying that the former is more strictly nocturnal (Werner 1969). Aktograph studies of Frankenberg (1977:16–17) also indicate that *petrii* may be more nocturnal than *sthenodactylus*, at least in spring. Moreover, individuals of *S. sthenodactylus* have been observed in the field in autumn and winter out in the open in daytime (E. Frankenberg 1977:79, personal communication). Among the scincids, there is some evidence that *Scincus* is diurnal, whereas the somewhat smaller *Sphenops* is nocturnal. Among the lacertids, the adult *Eremias* is only as large as a juvenile *Acanthodactylus*. Of the lizards, only *Agama savignii* is known to eat plant material in addition to insects. Among the snakes, both *Lytorhynchus* and *Cerastes vipera* prey on lizards, but the much broader head and the venomous character of the latter presumably facilitate a much wider scope of food items.

In addition to these arenicolous species, a number of more euryoecious species, particularly snakes, are also found in these sands. *Stenodactylus sthenodactylus*, *Coluber rogersi*, *Spalerosophis diadema*, and *Psammophis schokari* are probably most frequently encountered but others, including *Walterinnesia aegyptia*, also occur.

A special example is *Chamaeleo chamaeleon*, which lives in bushes and grass clumps in the dunes, but it is hardly a psammophile in terms of adaptation to locomotion on sand. The toad, *Bufo viridis*, and the climbing geckos, *Hemidactylus turcicus* and *Tarentola mauritanica*, occur in suitable mesic niches within the dunes.

Conclusions

This survey of Sinai carried out in 1956–57 and 1967–77 greatly increased our knowledge of the herpetofauna of this once relatively poorly known corner of the Near East. The herpetofauna of the Sinai Peninsula comprises at least 50 and possibly some 60 terrestrial reptile species, 4 marine turtles, and 1 toad. None of the species is completely endemic to the territory of Sinai. Each occurs in at least a small portion of at least one of the adjacent territories: the Negev desert of Israel, the Transjordanian desert, and the Eastern Desert of Egypt. Certain additional species, known from either or both Egypt and Israel, may yet be discovered in Sinai.

The literature records of several species from Sinai may be erroneous, and those of some others may yet be confirmed. The sand dunes of northern Sinai support a community of 10 Saharan psammophile reptile species, each representing a separate family or a genus of distinctive body size. Resource partitioning is apparent between some species. Most of these psammophiles are replaced by vicarious species both on disjunct sand areas and on adjacent non-sand soils. Several additional euryoecious species, mostly snakes, also occur in the same dunes.

Acknowledgments

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The Herpetological Components of Florida Sandhill and Sand Pine Scrub Associations

by

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Abstract

Investigations of the herpetofauna of the peninsular Florida sandhills and sand pine scrub revealed a diverse complex composed of a minority of xeric-adapted species combined with an array of wide-ranging and aquatic species that can be found in many Florida habitats. The xeric-adapted species required sand for burrowing or sand-swimming. The tortoise (*Gopherus*) digs burrows that serve as shelter for several other species; the wide-ranging generalist species, however, require none of the specialized conditions of the sandhills and scrub. Sand scrub, especially early successional stages, contains 22 species of reptiles and amphibians, which is more than in any other of a wide range of peninsular Florida habitats. Apparently the herpetofauna is responding to the dry, well drained soil and patches of sand free from roots rather than to any aspect of the vegetation. The sand swimming species (*Eumeces egregius*, *Tantilla relicta*, and *Neoseps reynoldsi*) depend on periodic disturbance (e.g., fire and clear-cutting) to remove the matted understory and pine canopy. The widespread distribution of these forms attests to the continuous presence, throughout history, of a mix of successional stages in both the sandhills and sand pine scrub.

The sandhill and scrub pine plant associations are characteristic and well defined elements of the Florida environment. Although vegetatively distinct, they are closely related physically and geographically (Fig. 1) and have very similar herpetofaunas. Autecological studies of sandhill and scrub species are available (Telford 1959; Jackson 1972; Smith, this volume), but, in contrast to extensive literature on the vegetation, previous research has not dealt with the community of animals living in these plant associations. The sandhills and sand pine scrubs, along with xeric hammocks, form the principal habitats in Florida for a distinctive herpetofauna based on xeric-adapted forms.

We initiated studies (Florida Fish and Game Commission 1976) in these habitats in the spring of 1975 using the methods detailed elsewhere (Campbell and Christman, this volume). In 1976 we substantially increased our efforts in the various subtypes of sandhill and scrub in the Ocala National Forest in central Florida to determine the distribution and relative abundance of amphibian and reptile species in the various successional stages of sandhills and scrub.

Characterization of the Habitats

Sandhill Association

The sandhill association and its successional relations to other Florida plant associations have received considerable attention over the years (Laessle 1958), and there is general agreement on the physical and phytogeographic characteristics of the sandhills. References to the reptiles and amphibians occurring in the sandhills generally use the designators "High Pine" (Carr 1940) or "Longleaf-pine Turkey-oak" (Laessle 1942). Similar habitats, differing only slightly in

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[1] Deceased: Died at Gainesville, Florida, on 10 December 1981.

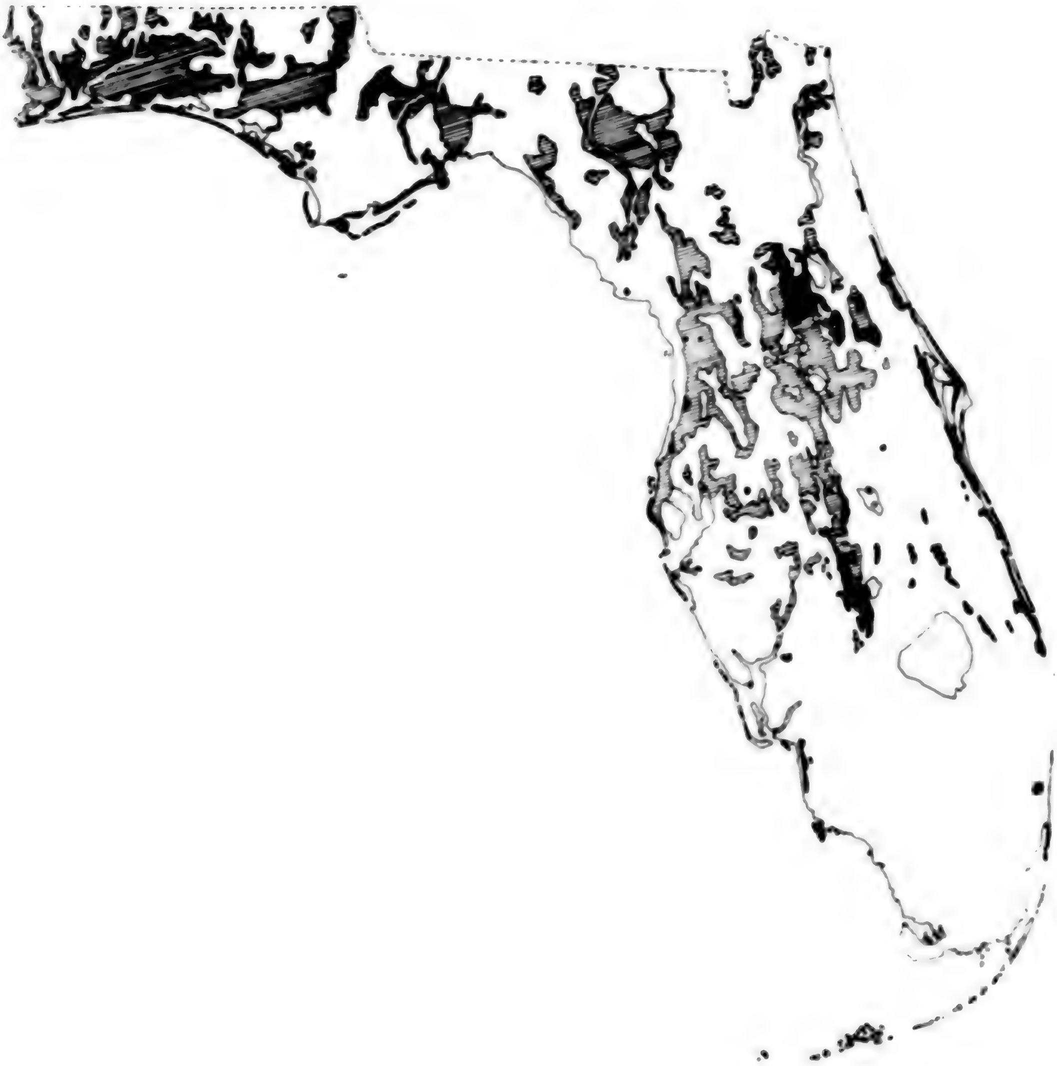

Fig. 1. Distribution of sandhills (hatched) and sand pine scrub (black) in Florida (Davis 1967)

their plant species, are found in scattered areas having suitable soils throughout the southern United States (Laessle 1958; Bozeman 1971), but the sandhills of the Florida peninsula support a herpetological community that is distinct from the sandhills of the Florida panhandle and other areas of the southeast. The following analysis will deal specifically with the peninsular sandhills.

Most sandhills in peninsular Florida occur on well-drained, sandy soils of the Lakeland series as defined by Gammon et al. (1953) and Laessle (1958). The physical characteristics of these soils and their similarity to the soils supporting sand pine scrub and xeric hammock, as well as the relative frequency of fire in these associations, are considered to be the factors determining which animals use these habitats. Sandhills are generally restricted to soils of slightly higher clay and silt content than those supporting the scrub association (Laessle 1958).

The sandhill association exists in two basic forms in peninsular Florida: the "typical" longleaf pine (*Pinus palustris*)/turkey oak (*Quercus laevis*) association, and the turkey oak sandhills. The typical phase is a three-tiered habitat with widely-spaced longleaf pines forming the upper level, an understory of scattered turkey oak (bluejack oak, *Q. incana*, may replace turkey oak on lower soils of the Blanton series), and a

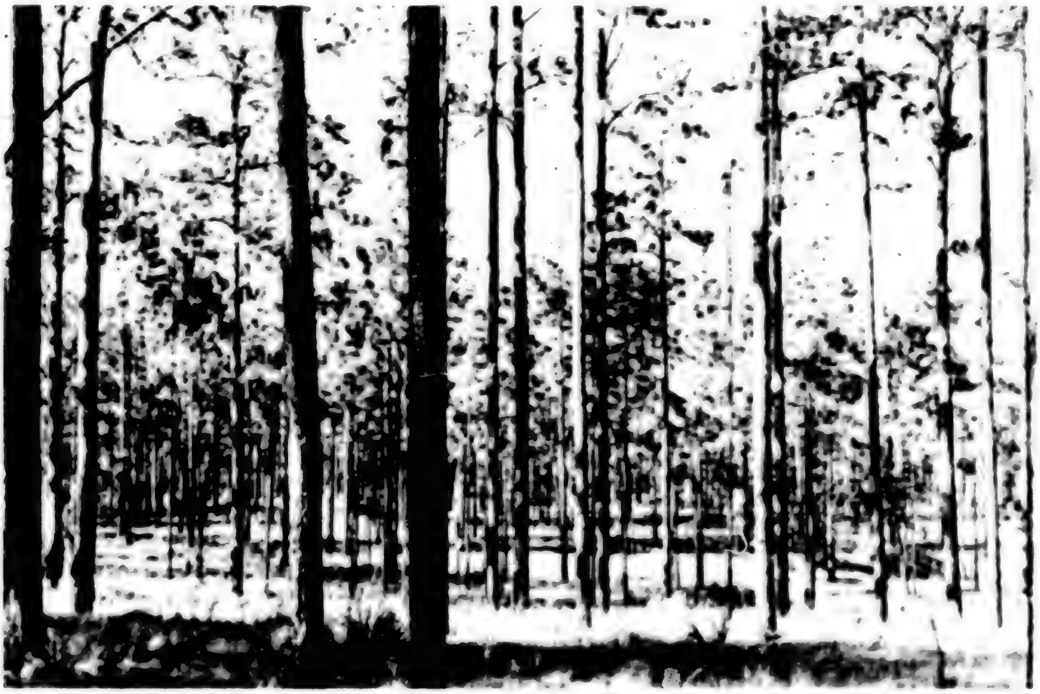

Fig. 2. Typical phase of the longleaf pine–turkey oak sandhill habitat in the Ocala National Forest, Florida.

ground cover dominated by wire grass (*Aristida stricta* and *Sporobolus gracilis*, Fig. 2). Fire is frequent in this habitat, perhaps the most widespread of the fire subclimax associations in Florida. The dominant plant species are fire resistant.

Where the longleaf pines are removed, the turkey oak increases in height, forming the canopy layer at 8–10 m, and the ground cover becomes less dense with frequent and extensive areas of bare sand interspersed with drifted piles of oak leaves and scattered vegetation (Fig. 3). Fire is also a frequent phenomenon in the turkey oak sandhill and often results in extensive areas of open sand and occasional damage to the oaks.

The turkey oak sandhill is by far the predominant phase of sandhill habitat remaining in peninsular Florida; lumbering demands on the longleaf pine long ago eliminated it over extensive areas of sandhill habitat. Today the Riverside Island area of the Ocala National Forest (Fig. 2) is perhaps the largest and least disturbed stand of the "typical" longleaf pine-dominated sandhill habitat remaining in the southeastern United States (Florida Game and Fresh Water Fish Commission 1976).

Sand Pine Scrub Association

The sand pine scrub association occurs throughout Florida in isolated patches, often associated with or adjacent to sandhills (Fig. 1). The soils that support scrub habitat are of the St. Lucie series and are essentially loose, unconsolidated sands, similar to but coarser and looser than those which support sandhills. There is never standing or running water in scrub habitats, as even the heaviest rains percolate immediately into the loose sand. Mulvania (1931: 528) referred to these soils as ". . . a bed of silica, to which the term soil is but remotely applicable." The Florida scrub has been called the ecological equivalent of the California chaparral (Laessle 1967).

Botanists have been intrigued with scrub since its description early in the last century (Vignoles 1823). Perhaps no plant community in Florida has stimulated more interest or more printed words (e.g., Vignoles 1823; Nash 1895; Whitney 1898; Harper 1914, 1921; Mulvania 1931; Webber 1935; Kurz 1942; Laessle 1942, 1958, 1967; Miller 1950; Cooper et al. 1959; Veno 1976).

Characteristic scrub tree species include the

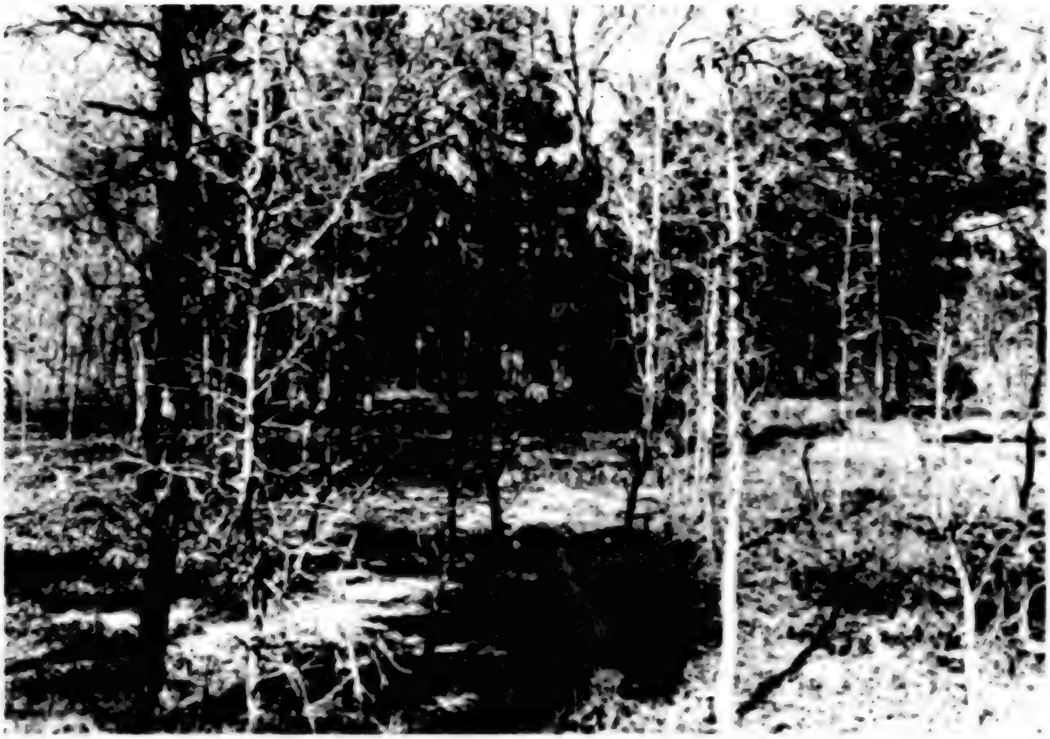

Fig. 3. Turkey oak phase of the longleaf pine–turkey oak sandhill habitat in the Ocala National Forest, Florida

sand pine (*Pinus clausa*), various evergreen oaks (*Quercus virginiana*, *Q. myrtifolia*, and *Q. chapmani*), and lyonia (*Lyonia ferruginea*). Scrubs can be divided into two major types: those with sand pine trees and those without. The latter are sometimes referred to as rosemary scrubs. It is not always clear why some scrubs lack sand pines. Where the pines have died of old age in the absence of fire, scrubs sometimes persist for many years (Laessle 1967). Other evergreen oak scrubs appear never to have had sand pines. The Florida scrub jay (*Aphelocoma coerulescens*), the sand skink (*Neoseps reynoldsi*), and the Florida scrub lizard (*Sceloporus woodi*) are largely restricted to the evergreen oak scrub without sand pines and to those scrubs with young sand pines.

Scrubs rarely burn but, when they do, the fire usually crowns, killing the sand pines. Under the extreme heat of a crowning fire, the sand pine seeds are released from the serotinous cones. More often than not, scrubs are adjacent to sandhill communities which burn frequently. Many authors have noted the tendency of ground fire in the sandhills to stop abruptly at the sandhill – scrub ecotone (e.g., Webber 1935; Laessle 1967). The dominant sandhill tree, longleaf pine, is well adapted to survive frequent ground fires which are readily kindled by the wire grass and deciduous oak leaves which accumulate rapidly. On the other hand, the evergreen oaks of the scrub provide little fuel for ground fires. Thus Webber (1935) referred to the scrub as a "fire fighting association." If fire is excluded from the scrub, the sand pines eventually die of old age and the habitat may ultimately succeed to hardwood (oak, magnolia) hammock (Veno 1976). When a scrub burns, however, the sand pines are killed, seeds are released, and the cycle begins again. At first there are extensive areas of open sand, but the vegetation gradually fills in to form an almost impenetrable tangle composed of a matted ground cover, a dense evergreen shrub layer, and a full pine canopy characteristic of a mature scrub.

Table 1. *Categories of reptile and amphibian species occurring in sandhills and scrubs in peninsular Florida.*

Characteristic

Xeric adapted
- *Eumeces egregius*
- *Neoseps reynoldsi*
- *Sceloporus woodi*
- *Masticophis flagellum*
- *Stilosoma extenuatum*
- *Tantilla relicta*
- *Cnemidophorus sexlineatus*

Wide-ranging
- *Scaphiopus holbrooki*
- *Gastrophryne carolinensis*
- *Bufo quercicus*
- *B. terrestris*
- *Rhineura floridana*
- *Anolis carolinensis*
- *Eumeces inexpectatus*
- *Scincella laterale*
- *Cemophora coccinea*
- *Coluber constrictor*
- *Micrurus fulvius*

Associated with Tortoise Burrows
- *Rana areolata*
- *Gopherus polyphemus*
- *Pituophis melanoleucus*

Frequent
- *Hyla femoralis*
- *H. gratiosa*
- *Ophisaurus compressus*
- *Diadophis punctatus*
- *Heterodon platyrhinos*
- *Lampropeltis triangulum*
- *Opheodrys aestivus*
- *Sistrurus miliarius*

Occasional
- *Hyla cinerea*
- *H. crucifer*
- *H. squirella*
- *Pseudacris ornata*
- *Ophisaurus attenuatus*
- *O. ventralis*
- *Sceloporus undulatus*
- *Drymarchon corais*
- *Elaphe guttata*
- *E. obsoleta*
- *Heterodon simus*
- *Storeria occipitomaculata*
- *Thamnophis sirtalis*
- *Crotalus adamanteus*

Associated with Aquatic Habitats
- *Acris gryllus*
- *Rana catesbeiana*
- *R. grylio*
- *R. sphenocephala*
- *Ambystoma talpoideum*
- *A. tigrinum*
- *Notophthalmus perstriatus*
- *N. viridescens*
- *Pseudobranchus striatus*
- *Siren intermedia*
- *S. lacertina*
- *Chrysemys floridana*
- *C. nelsoni*
- *Deirochelys reticularia*
- *Kinosternon bauri*
- *K. subrubrum*
- *Sternotherus odoratus*
- *Nerodia fasciata*
- *Seminatrix pygaea*
- *Thamnophis sauritus*
- *Agkistrodon piscivorus*

Results

General

Several distinct groups of amphibian and reptile species occur in the sandhills and scrub (Table 1): those that can be considered to be highly adapted to a xeric, sandy habitat (i.e., reaching maximum population levels or found only there); those that occur throughout a wide habitat spectrum; those species associated with burrows of tortoise (*Gopherus polyphemus*); and those species that occur in or near aquatic habitats surrounded by sandhills, scrub, or any other terrestrial habitat.

All of the xeric-adapted species except the Florida scrub lizard require loose, well-drained sand for burrowing or sand-swimming. *Gopherus* and associated species are also dependent on sandy soils for burrows. These species are restricted to sandhill, scrub, and xeric hammock habitats, although *Tantilla relicta* may rarely occur in more mesic habitats. *Gopherus polyphemus* deserves special mention as a focal species in providing burrow refuges for a wide variety of other species including *Rana areolata* and *Pituophis melanoleucus*, which are essentially restricted to this microhabitat in peninsular Florida. *Drymarchon corais*, generally considered a characteristic gopher tortoise burrow inhabitant, is not so restricted in peninsular Florida and may actually reach greater population levels in certain more mesic hardwood habitats. Its close relation to gopher tortoise burrows and xeric habitats is encountered primarily at its range margins in Georgia and Alabama; in peninsular Florida the burrows are more commonly used by *Pituophis* and a variety of other snake species.

The aquatic species occurring in the sandhills and scrub may reach high population levels around appropriate habitat but are best considered fortuitous additions to the species list. The greatest number of species occurring in the sandhill and scrub habitats are ecological generalists which find suitable conditions in a wide variety of habitats. Unfortunately, we know too little of absolute population densities of amphibian and reptile species to be able to judge relative habitat quality for most species and thus cannot rank the value of sandhills and scrub to these generalist species. On inspection of Table 1, however, it is clear that the generalists are all species which require none of the specialized physical or vegetative conditions of the sandhill and scrub associations.

Scrub Species Diversity

The community of herpetologists in Florida has long been familiar with the scrub endemics (*Neoseps reynoldsi* and *Sceloporus woodi*), but when our data showed that scrubs had the highest amphibian and reptile species richness of 11 terrestrial habitat types sampled (Table 2), we decided to look more closely at what Carr (1940:8) called, ". . . undoubtedly the most rigorous habitat in Florida . . . ."

We list 43 nonaquatic species of amphibians and reptiles as known to occur either characteristically, frequently, or occasionally in Florida scrubs and sandhills (Table 1). Two of these, *Neoseps reynoldsi* and *Sceloporus woodi*, are primarily restricted to scrub habitat. Others (e.g., *Eumeces egregius*, *Eumeces inexpectatus*, *Cemophora coccinea*, *Tantilla relicta*) may reach their greatest abundance in some successional stage of the scrub habitat. Still others occur in scrub only near its ecotone with sandhills or along roads through the scrub (e.g., *Gopherus polyphemus* and its symbionts).

Table 2. *Results of the herpetological trapping program by habitat type, Cross Florida Barge Canal Wildlife Restudy.* Eleutherodactylus planirostris, *an exotic species, has been omitted.*

Habitat type	Total number of species	Number of individuals array day
River swamp	3	0.05
Slash pine flatwoods	7	0.07
Longleaf pine flatwoods	16	0.13
Pond pine flatwoods	6	0.17
Hydric hammock	17	0.23
Mesic hammock	12	0.21
Xeric hammock	10	0.15
Longleaf pine sandhills	13	0.22
Deciduous oak sandhills	16	0.11
Evergreen oak scrub	21	0.16
Sand pine scrub (mature)	19	0.14

The reptiles that inhabit the scrub proper fall into two categories: those that "swim" beneath the sand surface (Mosauer 1932) and those that run on the surface of the sand. Even lizards such as *Anolis carolinensis* and *Sceloporus woodi* spend much time on the surface, as pit-fall records indicate. *Neoseps reynoldsi*, *Eumeces egregius*, and *Tantilla relicta* are the principal sand swimmers, although other small species are frequently encountered beneath the sand surface (e.g., *Scincella laterale*, *Lampropeltis triangulum*, *Heterodon platyrhinos*). Smith (this volume) investigated the details of the niches of the three principal sand-swimming species.

Amphibians are poorly represented in the scrub. *Notophthalmus perstriatus* efts occasionally inhabit the scrub. Only the most xeric-adapted anurans will be found regularly in true scrub. Turtles are essentially lacking, although *Kinosternon bauri* may occasionally wander through scrubs, and *Gopherus polyphemus* will occur near roads and ecotones where the soil will sustain burrow construction. Snake and lizard diversity is high.

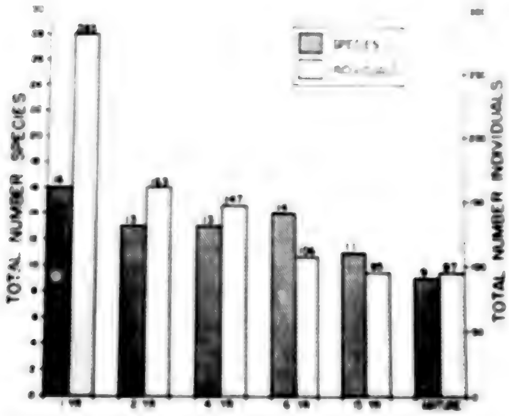

Fig. 4. Total numbers of species and individuals of reptiles and amphibians collected in various ages of sand pine scrub in the Ocala National Forest, Florida.

Scrub and Sandhill Succession

Our ongoing trapping program in the Ocala National Forest was designed to determine if there are any differences in the terrestrial herpetofauna between different-aged stands of sand pine scrub and between the facies of the sandhill association. We installed two standardized trapping arrays in turkey oak and longleaf pine sandhills and in each of six various-aged stands of even-aged sand pine. During the first 10 months of this sampling, we collected 891 specimens of 22 species in the scrub traps (Fig. 4). These results suggest strongly that some species are more abundant in the younger stands of scrub while others are more abundant in the more mature scrubs. No species is confined to the more mature scrubs, although several species collected in the younger stands have not been taken in the mature scrub. Of 22 species collected, only *Anolis carolinensis*, *Scincella laterale*, and possibly *Eumeces inexpectatus* are more abundant in the older scrubs. On the other hand, at least six species occur more frequently in the younger scrubs. Notable among these are *Scaphiopus holbrooki*, *Cnemidophorus sexlineatus*, *Sceloporus woodi*, and *Tantilla relicta*. The 1-year, 2-year and 4-year-old sites have thus far produced 593 specimens of 20 species, whereas the 6-year, 15-year, and mature sites have yielded only 298 specimens of 16 species. A similar pattern characterized the turkey oak and longleaf pine sandhills. We believe that additional collecting will not appreciably change this trend; that is, it appears that species richness and animal abundance decrease as the pines mature or, to be more specific, as the ground cover increases.

Discussion

It appears to us that the amphibian and reptile fauna occurring in the sandhills and scrub is not actually responding to a particular plant association, but rather to the physical characteristics of the habitat. Where these physical characteristics are met in other plant associations (e.g., xeric hammock), many of the same vertebrate species occur. Thus the scrub lizard and the sand skink are really adapted to habitats that are dry, well-drained, and offer patches of open sand, free from rooted vegetation. We can think of no amphibian or reptile species in Florida that has a distribution restricted to a single plant association. Actually, we argue that the plant species occurring in a given habitat are responding to many of the same environmental factors as the animals. Perhaps wildlife habitats should be classified according to the significant physical characteristics to which both the plants and the animals are adapted rather than by plant associations. The present system can lead to misleading judgments, and we offer a single example: the Florida gopher tortoise is known from several "habitats" (i.e., plant associations): longleaf pine sandhills, deciduous oak sandhills, evergreen oak scrub, sand pine scrub, xeric hammock, dry flatwoods, and a host of ruderal situations. Does this mean that the gopher tortoise is a highly-adaptable, ubiquitous species? It does not. Gophers are essentially restricted to habitats with well-drained, sandy soils, and an abundance of grasses and forbs, and ultimately, with maximal light intensity at ground level (Auffenberg and Franz 1980). These conditions can be met in a variety of places regardless of the specific plant species living there.

A comparison between longleaf pine and turkey oak sandhill may shed light on the evolution of the highly adapted sandhill and scrub reptile and amphibian species. Aside from the presence or absence of a pine canopy and the corresponding dwarfing or enlargement of the understory oaks, these facies of the association are strikingly different in the nature of the ground cover. The

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longleaf pine-dominated sandhill usually supports a dense ground cover of wire grass and forbs, whereas the turkey oak-dominated facies is more open, often with extensive areas of bare sand, and it receives more intensive surface insolation. The reptiles characteristic of the sandhills are, as noted, species which burrow and highly specialized sand "swimmers." Species such as *Tantilla relicta*, *Eumeces egregius*, and *Neoseps reynoldsi*, which require loose sand for sand swimming, historically have encountered such conditions in the sandhills only in areas of disturbance, such as the burrow mounds of *Gopherus polyphemus* and *Geomys pinetis*, or the open areas resulting from fire, especially under a turkey oak canopy. In the longleaf pine turkey oak association such conditions (minus man's imposition of road shoulders and other disturbances) are localized islands of loose sand protruding from a cover of wire grass. Similarly, the mat of roots and humus covering the sand in the mature sand pine scrub would require breaks to provide suitable conditions for these species.

Neoseps reynoldsi, *Eumeces egregius*, *Tantilla relicta*, and *Stilosoma extenuatum* are also more abundant in early successional stages of sand pine scrub than they are in the advanced stages with a full pine canopy, dense evergreen shrub layer, and matted ground cover. To provide conditions for the evolution of the endemic or characteristic species of the sandhills and scrub, there must have always been such disturbed areas where loose surface sand was available. Despite the contention that the central sandhills of Florida were historically blanketed by a sheet of longleaf pine turkey oak (Laessle 1958), it would appear more probable that a mix of successional stages, both in sandhills and sand pine scrub, has always existed. Breaks in the typical or mature stages of both habitats could, and probably did, result from severe fires, tornado or hurricane blow-downs of the canopy trees, outbreaks of pine-bark beetles, or other natural disasters. These factors would have maintained a mix of habitats amply supplied with the open, loose sand conditions needed for the evolution of the unique herpetological components of the peninsular Florida sandhill and scrub associations. These species, especially *Neoseps reynoldsi*, *Tantilla relicta*, and to a lesser extent, *Eumeces egregius*, are thus cast as "weed" species, colonizers of a patchy early successional or disturbed habitat type which occurs throughout the sandhill, sand pine scrub, and xeric hammock vegetative associations as a result of biological (*Gopherus*, etc.) or catastrophic (fire) factors.

Although most of the highly adapted scrub and sandhill fauna meet few or none of the biological requirements typically cited for colonizing species (see Baker and Stebbins 1965), they must be considered colonizers because of the short-lived nature of their required habitat. A population of sand skinks cannot persist to its maturity in a patch of sand pine scrub; they invade young scrubs opened by killing fires, scrubs without sand pine, and sandhills without wire grass and longleaf pines. Just how a species with a reproductive rate of only one or two young per female per year (Telford 1959) and such apparently poor vagility can do this is a question worth pursuing.

In our current study of the scrubs of the Ocala National Forest, we consistently trapped more species and more individuals in the younger sand pine scrubs. This suggests that there are either more animals in the younger stands or that those present are easier to trap. It is clear that the recently clear-cut scrub is more frequently used by "typical" scrub species; when we consider the natural history of scrub (i.e., fire ecology), this makes sense. It should come as no surprise that the scrub-adapted fauna is accustomed to survival in even-aged stands of sand pine. It thus appears that clear-cutting and even-age management of sand pine stands may mimic the natural situation of infrequent crown fire to which the scrub fauna is adapted.

The variables of a herpetological association or "community" in the scrub and sandhills habitat are difficult to define. Many of the most common species are broadly distributed and only fortuitously juxtaposed in the sandhills and scrub; the more specialized species occur only in restricted microhabitats. With only a few exceptions, the species list for these areas can be duplicated in various other habitat types in peninsular Florida. If we exclude aquatic habitats, the species list is virtually identical to that for xeric hammock.

It appears evident from these data that the concept of a herpetological association or "community" cannot be defined along plant association boundaries in the xeric habitats of peninsular Florida. The local distribution of species is determined by a complex of physical and probability factors at least partially independent of the plant species of the area. The most heuristic approach is to view amphibian, reptile, and plant species as responding to a similar set of physical and biotic factors without assuming any interdependency between species. If the definition of a herpetological "community" is to be more than the fortuitous association of a group of individuals of a variety of species at a specific place and time, we must look beyond the plant association. In the xeric habitats of peninsular Florida, the particular plant associations appear less important than the presence or absence of areas of loose dry sand.

Acknowledgments

The staff of the Ocala National Forest have been of immeasurable assistance to our studies at all levels, from the initial planning stages to the frequent extrication of vehicles from beds of soft sand. Mrs. W. Guerrero, B. Knowles, and R. Roth should especially be mentioned. C. R. Smith deserves special thanks for his faithful efforts in running the trap lines under the best and worst of conditions. Howard Kochman and W. S. Lippincott helped in a variety of important capacities throughout the study.

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Food Resource Partitioning of Fossorial Florida Reptiles

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Abstract

Tantilla relicta, *Eumeces egregius*, and *Neoseps reynoldsi* share the same habitat within the scrubs and sandhills of central Florida. Stomach analyses of specimens from several localities show considerable differences in their arthropod prey. *Tantilla relicta* inhabits surface litter and specializes on tenebrionid larvae. *Eumeces egregius* is a surficial skink which generalizes on blattids, crickets, and spiders. *Neoseps reynoldsi* possesses an anatomy specialized for subsurface "sand swimming" and takes a variety of prey, including termites, tenebrionid larvae, spiders, and antlions. The food resource overlap of *Neoseps reynoldsi* with the other two species is apparently reduced by its adaptations to a subsurface microhabitat.

Tantilla relicta, *Eumeces egregius*, and *Neoseps reynoldsi* are fossorial, insectivorous squamates which occur sympatrically within the scrubs and sandhills of central Florida. The food habits of *T. relicta* and its relationship to the two lizard species in their common habitats are unknown.

The sand skink, *Neoseps reynoldsi*, has the wedge-shaped snout, counter-sunk jaw, and drastically reduced limbs of a highly specialized "sand swimmer." Cooper (1953) and Myers and Telford (1965) provided the only published references to the sand skink's diet. *Eumeces egregius*, the mole skink, has a more generalized anatomy with typical limbs but also swims through the sand. Its food habits are reported in Hamilton and Pollack (1958) and Mount (1963). *Tantilla relicta*, the crowned snake, also possesses the wedge-shaped head and counter-sunk jaw which permit efficient sand-swimming. No published reference to the prey items of this species exists, but literature on the food of *T. coronata* (Hamilton and Pollack 1956) and *T. gracilis* (Force 1935) is available.

Methods and Materials

The Cross Florida Barge Canal Restudy (Florida Game and Fresh Water Fish Commission 1976) and a current study in the Ocala National Forest, Marion County, Florida, by the National Fish and Wildlife Laboratory provided the bulk of examined specimens. A few additional *N. reynoldsi* were also used.

Pitfalls and funnel traps in conjunction with drift fences (Campbell and Christman, this volume) constituted the primary collection technique. In the Ocala study, 20 arrays with four fences each were emplaced in July 1976 and checked weekly through December 1977. The 10 Ocala study sites, each with two arrays, included turkey oak (*Quercus laevis*) and longleaf pine (*Pinus palustris*) sandhills, evergreen oak scrub, and various ages of sand pine (*Pinus clausa*) scrub from clearcut to mature stand. The Barge Canal study traps involved from one to four arrays in each of the 11 following habitats: turkey oak and longleaf pine sandhills; evergreen oak and sand pine scrub; hydric, mesic, and xeric hammocks; longleaf pine, slash pine (*Pinus elliottii*), and pond pine (*Pinus serotina*) flatwoods; and mixed swamp. The trapping at the Canal site began in spring 1975, sampling periods were 1 to 2 weeks, and trapping was concluded in December 1975. All trap sites were in or adjacent to the Ocala National

Forest with the exception of a turkey oak sandhill located 24 km southwest of Ocala and 14 km east of Dunnellon. In addition to the arrays, more conventional field work supplied further material for examination. All specimens were frozen the day of capture for later preservation.

The scrubs and xeric hammock are upland habitats associated with an extensive paleodune field of infertile silicious sand with high internal drainage. The Ocala scrubs occur on whitish sands of the St. Lucie and Lakewood series (Laessle 1958). Vegetation includes sand pine, myrtle oak (*Quercus myrtifolia*), saw palmetto (*Serenoa repens*), rosemary (*Ceratiola ericoides*), and lichens (*Cladonia* spp.). As sand pine scrub matures, the shrubby understory and ground litter become more extensive. Campbell and Christman (this volume) describe sand pine scrub regeneration. If no regenerative mechanism occurs, the sand pines may decline due to senescence and the area may succeed to evergreen oak scrub or xeric hammock. Small oaks such as the myrtle oak dominate the evergreen oak scrub and open patches of sand develop between clumps of the oaks and rosemary bushes. A slightly moister soil probably gives rise to xeric hammock dominated by live oaks (*Quercus virginiana*).

The well-drained upland sandhills occur on yellow infertile sands of the Lakeland series. Longleaf pine, turkey oak, wild persimmon (*Diospyros virginiana*), live oak, and two wire grasses (*Aristida stricta* and *Sporobolus gracilis*) commonly occur in sandhills. When the pine trees are lumbered, turkey oak dominates the sandhill, herbaceous ground cover is reduced, and open patches of sand develop. These disturbed sandhills approach scrub conditions with a consequent reflection in their faunal assemblages (Campbell and Christman, this volume).

The mesophytic and hydrophytic sites are characterized by much poorer drainage than the scrubs and sandhills mentioned above and the data confirmed the virtual absence of the three species of squamates in these areas. For this reason, habitat descriptions are omitted here and the reader is referred to Snedaker and Lugo (1972).

In all, 219 *Tantilla relicta*, 164 *Eumeces egregius*, and 14 *Neoseps reynoldsi* were available for examination of stomachs. The Barge Canal study totals included six *T. relicta* and two *N. reynoldsi* which were caught by hand. In addition, four *N. reynoldsi* from the Sebring area in Highlands County were examined.

The stomach and intestinal contents of all of the specimens were removed and placed in small vials containing 75% isopropyl alcohol. The contents of each vial were placed in a petri dish under a variable power (7–30X) dissecting scope, segregated and identified according to Chu (1949) and Borror and DeLong (1964). Only the number and frequency of different food items were recorded.

Results

A number of factors were analyzed for each species, including spatial and temporal activity or presence, adaptations, and food habits. Habitat and microhabitat preferences comprised the spatial component. Seasonal activity was plotted from July 1976 to December 1977 to determine any temporal differences between the three species.

Habitat Preference

Tantilla relicta was common in the longleaf pine and younger stands of sand pine scrub. Turkey oak sandhill, xeric hammock, and the drier evergreen oak scrub had moderate populations. Specimens were trapped rarely in the wetter evergreen oak scrub site. *Eumeces egregius* was taken commonly in the turkey oak sandhill, most younger sand pine scrubs, and evergreen oak scrub. The mature sand pine scrub, longleaf pine sandhill, and xeric hammock arrays trapped few or none, but occasional individuals were collected by hand from all of these habitats. *Neoseps reynoldsi* was trapped rarely and only in the Ocala turkey oak sandhill.

Annual Activity

Seasonal variation in numbers was plotted to determine any temporal activity differences in the three species (Figs. 1 to 3). The initial high values in Figs. 1 and 2 resulted from trapping a previously undisturbed population. Thereafter the values leveled off to a true reflection of activity. Peaks of activity occurred in the September–October and March periods, and inactivity

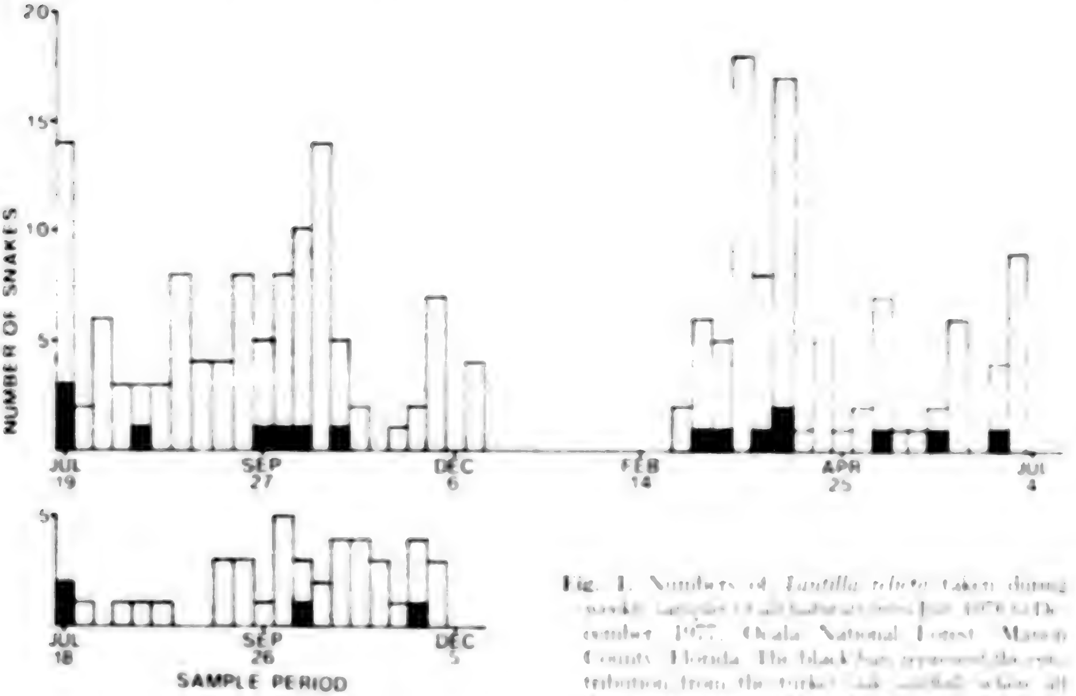

Fig. 1. Numbers of *Tantilla relicta* taken during weekly samples of all habitats from July 1976 to December 1977, Ocala National Forest, Marion County, Florida. The black bars represent the contribution from the turkey oak sandhill where all three species occurred together.

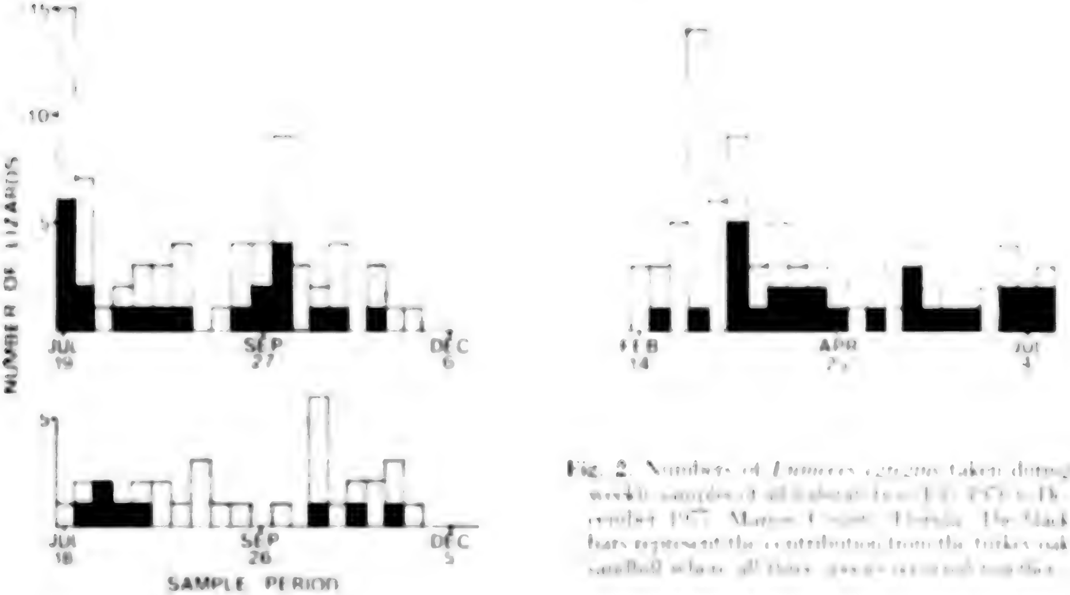

Fig. 2. Numbers of *Eumeces egregius* taken during weekly samples of all habitats from July 1976 to December 1977, Marion County, Florida. The black bars represent the contribution from the turkey oak sandhill where all three species occurred together.

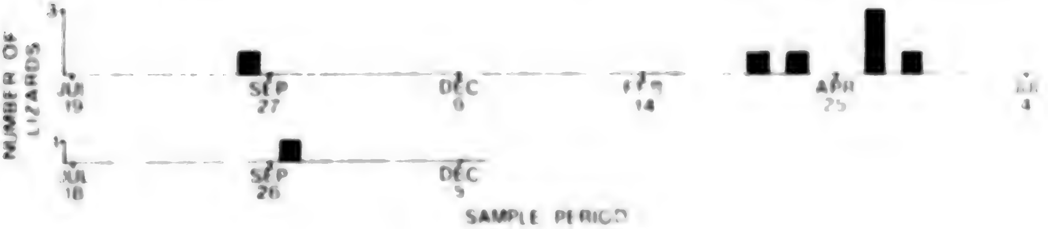

Fig. 3. Numbers of *Neoseps reynoldsi* taken during weekly samples of the turkey oak sandhill from July 1976 to December 1977, Marion County, Florida.

Table 1 *Numbers and percentage frequency of occurrence of 270 prey items in 124 stomachs of* Tantilla relicta *from Marion County, Florida, 1975–77.*

Prey items	Number of prey items	Percent of prey items	Number of stomachs	Percent frequency of occurrence
Tenebrionidae (larvae)	242	89.6	106	85.5
Chilopoda	17	6.3	16	12.9
Gastropoda	6	2.2	5	4.0
Insecta (eggs)	5	1.9	4	3.2

set in from December to February. Trapping for the 5 month period in the second year showed a reduction in the absolute numbers of animals taken, but the activity levels remained essentially the same for corresponding times of year. The *Neoseps reynoldsi* and turkey oak sandhill data seemed to follow these general trends. No temporal differences in activity appeared between the three species.

Food Habits

Identifiable food occurred in 124 (56.6%) of 219 *Tantilla relicta*, 83 (50.6%) of 164 *Eumeces egregius*, and 9 (61.3%) of 14 *Neoseps reynoldsi*. Mount (1963) found 257 (55.9%) of his 460 *E. egregius* with identifiable food. Even though some of the trapped *E. egregius* were probably restricted to a trap for a week or more, they apparently ate selectively of what happened into the traps, and avoided changing their diets or increasing the percentage of empty stomachs. Comparison of stomach contents from *T. relicta* and *N. reynoldsi* with published records and with food data from hand-caught specimens showed that they also did not change their diets significantly on being trapped. No differences in diet composition were observed between different habitats or times of year for a particular species. Whether an animal was caught in a funnel trap, in a bucket, or by hand made no difference in food items found in their stomachs.

The feeding strategy of *Tantilla relicta* was specialized to the extent that the larva of what is apparently one species of tenebrionid beetle occurred in 85.5% of stomachs with food and made up 89.6% of the numerical total. Centipedes and snails were found only in *T. relicta* and accounted for almost all of the remainder of its diet (Table 1). The diet of *T. relicta* differs from those of *T. gracilis* and *T. coronata*. Force (1935) wrote that *T. gracilis* ate mostly centipedes, along with noctuid, elaterid, and tipulid larvae. Hamilton and Pollack (1956) found that *T. coronata* also fed mostly on centipedes, and occasionally on coleopterous larvae, blattids, and millipedes.

Eumeces egregius fed largely on roaches, spiders, and crickets and on minor amounts of termites, adult and larval beetles, dipterans, sawflies, ants, insect eggs, and earwigs. *Neoseps reynoldsi* stomachs contained primarily beetle larvae, spiders, termites, and antlions.

Food habits comparison between the three species (Table 2) showed two major areas of overlap. Both *T. relicta* and *N. reynoldsi* relied heavily on coleopterous larvae. Conversely, tenebrionid and elaterid larvae were present in

Table 2 *Percentage of total prey items and frequency of occurrence of prey groups in stomachs of* Neoseps reynoldsi *(n = 9),* Eumeces egregius *(n = 83), and* Tantilla relicta *(n = 124). Marion County, Florida, 1975-77.*

	N. reynoldsi		*E. egregius*		*T. relicta*	
Prey group	Percent occurrence	Percent total items	Percent occurrence	Percent total items	Percent occurrence	Percent total items
Coleopterous larvae	33.3	13.3	6.0	4.4	85.5	89.6
Rhinotermitidae	22.2	63.3	2.4	2.2	0.0	0.0
Orthoptera	0.0	0.0	63.9	43.8	0.0	0.0
Arachnida	33.3	10.0	43.4	28.5	0.0	0.0

only 6.0% of the *E. egregius*. The other area of overlap was spiders, which were taken in large numbers by both *N. reynoldsi* and *E. egregius*. Roaches and crickets completed the bulk of the diet of *E. egregius*. Termites and antlions occurred in 22.2% of *N. reynoldsi* stomachs with food, but were rarely found in guts of the other two species.

Discussion

None of these three species appear to be a general insectivore, which indicates that natural selection probably has fashioned animals that feed on particular prey in particular microhabitats. The relative abundance of each species probably is not reflected accurately by the Ocala trap data. Pitfalls and funnel traps, by virtue of their construction, tend to trap mostly surficial animals, causing arboreal and burrowing species to be underrepresented. Because of its sand-swimming specialization, *Neoseps reynoldsi* has less chance of being trapped than either *Tantilla relicta* or *Eumeces egregius*. In view of normal field collection data, however, *N. reynoldsi* appears to be considerably less abundant than the other two reptiles. The data support the contention that *E. egregius* is one of the commonest lizards and *T. relicta* is the commonest snake in most of the scrubs and sandhills.

The presence of *Neoseps reynoldsi* in the Ocala turkey oak apparently results from a peculiar set of circumstances. Very small populations probably exist in the scrub, as evidenced by a few specimens collected from this habitat at Central Tower and just north of the junction of Pipeline Road (FR 97) with SR 316 (S. P. Christman, personal communication). After lumbering for longleaf pine, a sandhill may approach the substrate conditions of evergreen oak and young sand pine scrubs, which comprise the preferred habitats for *N. reynoldsi* south of the Ocala Forest. This process seems to have occurred in the Ocala turkey oak; both *N. reynoldsi* and sand pines subsequently colonized from the surrounding scrub. In the past when extensive wildfires (14,200 ha burned in 4 h in 1935) reduced the Ocala sand pine forest to a few patches of mature trees surrounded by large regeneration areas, *N. reynoldsi* was probably as abundant as in its unmanaged habitats south of the Ocala Forest today. Within the Ocala Forest, *N. reynoldsi* is marginally abundant in the extensive man-induced turkey oak sandhills and very rare in the surrounding scrub.

Food habits reflect microhabitat. Centipedes and snails tend to be superficial in surface litter, whereas termites and antlions are more subterranean. *Tantilla relicta* is found most frequently by raking sand during the day, but this probably reflects its habits at a time when it is not feeding. Considering its chilopodan and gastropod prey, it probably feeds at or above the surface. In view of its food habits and specialized adaptations, *Neoseps reynoldsi* apparently feeds and spends most of its time below the surface. Sand skinks probably take spiders in their own burrows. Telford (1959) collected all but 2 of over 60 *N. reynoldsi* from 5 to 10 cm below the surface. At the turkey oak sandhill trap site, one individual was taken on the surface of an open patch of sand at 1300 h on a sunny day. However, about 20 other specimens were collected by raking them out of the sand. Telford (1959) wrote that his captives fed mostly below the surface.

Eumeces egregius has more generalized food habits than either *Tantilla relicta* or *Neoseps reynoldsi* and seems to take anything small enough to overpower. Moreover, Mount (1963) stated that the Cedar Key Airstrip Island and Seahorse Key populations fed on amphipod cructaceans and dermapterans, respectively. Clearly, *E. egregius* is an opportunistic feeder. Most of its food items are surficial species, and Mount (1963) stated that the data "suggest that most of its food is captured in sheltered situations, perhaps in pre-existing subterranean passages." A reference from Wright and Wright (1957) alluded to all three species. They repeat field notes from O. C. Van Hyning, who had airport workmen at Eustis watch carefully while they were grubbing. Van Hyning wrote, "They took *Tantilla* in the surface layer, *Eumeces egregius* near the surface, but *Neoseps reynoldsi* and *Rhineura* six to ten inches or more down."

Food seems to be the major potential source of competition between these three species, and natural selection apparently has caused such competition to be diminished through microhabitat and dietary differences. *Eumeces egregius* avoids possible food competition by possessing a diet suited to its adaptations as a relatively generalized lizard and by feeding in its near-surface microhabitat. *Tantilla relicta* specializes on a prey which is unimportant to *E. egregius*, permitting coexistence of both in surficial microhabitats. The food items of *Neoseps reynoldsi* overlap those of both *E. egregius* and *T. relicta*, but competition apparently is reduced by the specialization of *N. reynoldsi* to a completely subterranean existence. *T. relicta* and *E. egregius* are also sand-swimmers. However, this locomotion is probably reserved for different activities than feeding. By swimming in the sand, these three species can escape predation, avoid inhospitable weather, and thermoregulate in exposed sandpiles, such as mounds of the pocket gopher (*Geomys pinetis*) and gopher tortoise (*Gopherus polyphemus*). The dietary differences of these animals indicate that none but *N. reynoldsi* feeds while sand-swimming. The differences in microhabitat and food preferences apparently permit these three species to coexist in the same habitats and to efficiently use the available food resources.

Acknowledgment

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TECHNIQUES OF COMMUNITY ANALYSIS

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Tracking as an Aid in Ecological Studies of Snakes

by

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Abstract

Snakes leave identifiable impressions when crawling over fine-textured soils. Therefore, dirt roads, dunes, and surfaces prepared by abrading topsoil have been used as trackways in ecological studies of snake populations in chaparral and desert in southern California. Preliminary data point to the usefulness of snake tracks in determining relative or behavioral densities, spatial relationships, social behavior, and species composition within communities. In desert sandy habitats, sidewinder rattlesnakes (*Crotalus cerastes*) have been followed for distances exceeding 1.2 km. In a montane chaparral community it was possible to distinguish tracks made by the three common species, *Crotalus viridis*, *Pituophis melanoleucus*, and *Masticophis lateralis*. Data for snake activity in chaparral point to the difficulties of determining the densities and comparative demographic features of snake populations.

Because of the difficulty of observing and capturing snakes, studies of their ecology have lagged behind that of other vertebrates. It is difficult, often impossible, to enumerate or estimate snake population densities, and community studies may suffer from the lack of equal information for species owing to differences in behavior, population density, and accessibility to the investigator.

Walter Mosauer was probably the first herpetologist to realize that tracks provided convenient records of snakes' activities and that trackways might be used profitably to supplement the scarce opportunities of actual observation. Snakes leave distinct, identifiable impressions when crawling on fine-textured substrate, and these tracks can provide information about the numbers of snakes in an area; time, rate, direction, and extent of movement; social behavior; species composition within a community; and, to some degree, individual recognition. Yet, apart from early descriptive studies, a tracking approach has not been widely applied in quantitative ecological studies by herpetologists (see Mosauer 1933; Cowles 1949; Bider 1968). In studies of other animals, most notably mammals, tracking methods have been adopted to determine home ranges and activity patterns, as well as to census populations. Population estimates based on tracking can be highly precise and are considered superior to estimates based on trapping alone (e.g., Marten 1972).

The intent of this paper is to stimulate interest in the development and application of tracking methodologies in ecological studies involving snakes. The discussion is aimed at identifying some potential applications of tracking methods in the light of two case studies in desert dune and montane chaparral ecosystems. I also comment on some of the difficulties of determining densities and demographic units within snake populations.

Sidewinder Studies at Kelso Dunes

The fine-grained sands of desert dunes provide unique opportunities for studying the daily movements of snakes, especially those of "sidewinder" vipers which occur (sometimes abundantly) in dune habitats of low latitude deserts.

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The following account is based on unpublished data from Brown (1970), who studied a population of *Crotalus cerastes* at Kelso Dunes in the Mojave Desert of southern California from June 1967 to June 1969.

The study area was a 7-ha grid of windblown sand at the easternmost edge of the Devil's Playground sand sea, roughly 4 km SSE of Kelso, San Bernardino County, California. The fine sand at this locality is 2 to 3 m deep but becomes progressively shallower to the east, where the dunes finally give way to the sloping alluvial fan of the Providence Mountains. A matrix of rather uniformly spaced creosote bushes (*Larrea divaricata*) form nuclei for prominent accretion dunes on the study grid proper; other vegetation comprises a denser assemblage of low-growing plants such as galleta grass (*Hilaria rigida*), burroweed (*Franseria dumosa*), and sandpaper-leaf (*Petalonyx thurberi*).

Sidewinder tracks are made as a progressive series of parallel impressions, each one terminating in the hook of a "J" (see Gans 1970). The hook is formed by the head of the snake and indicates the direction of travel. In ideal circumstances, the length of a track should exactly equal that of the sidewinder (Klauber 1956). However, a number of comparisons using snakes caught in the field showed that this was not always the case; most tracks varied from 3 to 5% shorter than the snakes which had made them. However, because this error is quite small, the tracks of this species can be used to determine the directions of movements of individuals and the size composition of a population.

Tracks at the Kelso study site were readily located by walking the length of the study grid in a series of parallel traverses in the early morning. Tracks may become obliterated or erased during the day due to wind and the unfavorable angle of sunlight. If any part of a trackway entered the grid, it was mapped for its entire length, thus providing detailed information on sidewinder movements. Trackways found outside the grid were also mapped for comparative data on length and direction. Frequently, the sidewinder that had made a given trackway was found and could be observed or captured. Metal rods were used to mark the start and finish points of trackways, and this allowed monitoring the progressive movements of individual sidewinders over periods of several days. For each trackway, both the total length and the straight-line distance from start to finish were recorded.

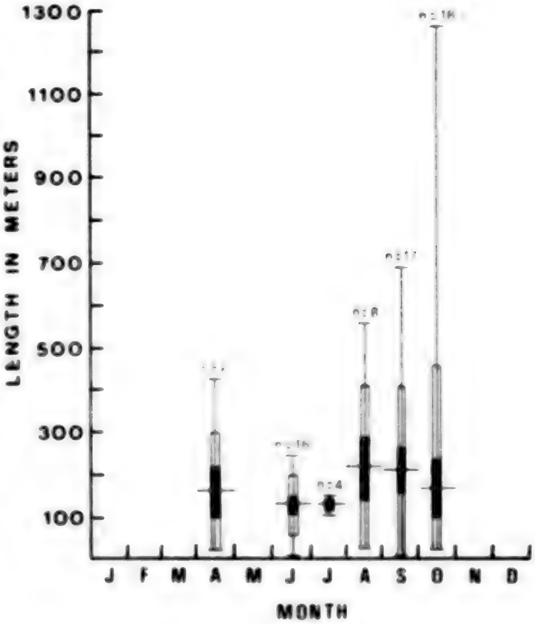

Fig. 1. Lengths of sidewinder trackways measured during 1967–69 on the Kelso study site, plotted by month. Vertical bars denote one standard error (black) and one standard deviation (white) on either side of the mean (horizontal line). (After Brown [1970], with permission.)

Tracks were found on the study site from April to October and provided a quantitative record of sidewinder activity during the two years of study. Trackways in June and July averaged somewhat shorter than those of earlier spring or fall; the longest trackways were recorded during the cooler months (Fig. 1). However, trackways of a given individual were not necessarily uniform in length or of increasing distance on successive nights. Nor was direction consistent, either for the population or for individuals. Occasionally, individual sidewinders moved long distances in short periods. For example, the longest trackway made by a sidewinder in a single night of wandering was that of an adult snake which on 13–14 October moved a total distance of 1,269.2 m. Few juvenile trackways were mapped, but they were said to be shorter than those of adults. The total length of a trackway usually was less than twice the straight-line distance between start and finish points.

Brown suggested that sidewinders probably wandered randomly without home ranges or with home ranges considerably larger than those of the few crotalids that have been studied intensively (e.g., Fitch and Glading 1947; Fitch and Shirer 1971). My own impressions during visits to Kelso Dunes were that sidewinders there typically followed the "path of least resistance" (e.g., between shrubs, in low places between accretion dunes, etc.) without purposeful exploration, as in cases where tracks progress from shrub to shrub or from burrow system to burrow system.

Some of the early observations of sidewinders were made by Mosauer (1933) who trailed these snakes over the sand dunes of the Coachella Valley, California. He found that the tracks made in a given night often would trend in a particular direction for as much as 305 m, and the snake was often found coiled at the base of a plant at the end of the track. Mosauer surmised that after a few nights of wandering the snakes possibly might return to their starting point. Brown's data fully support Mosauer's on the wandering inclinations of sidewinders and the distances they travel. However, only once was a sidewinder observed to return to its starting point after a night of wandering, and it seems doubtful that this occurs very often in this species. On the other hand, the western diamondback rattlesnake (*Crotalus atrox*), formerly found in the Coachella Valley along with the sidewinder, apparently does have a homesite to which it returns each morning (Mosauer 1935).

Studies on the 7-ha grid showed that from two to five trackways were found there daily from April to October. This indicates a variable surface density of from 0.29 to 0.71 active sidewinders per hectare. These figures are almost certainly underestimates of the actual population density on the Kelso Dunes, for a significant percentage of the population might not be active on the surface during a given measurement period. In Brown's study, the grid was worked by a single person, and it was difficult to follow individuals for long periods. Given sufficient manpower, however, it should be possible to follow the sequential movements of individual snakes over a significant period of the active season and enumerate directly the active population. Very likely the population on the 7-ha grid is largely transient and may fluctuate in density over rather short periods of time. This dynamic aspect of the population structure would be difficult to assess from conventional mark and recapture techniques.

A very important implication of the trackway studies at Kelso Dunes is that, given a randomly mobile population wherein some individuals elect to disperse relatively long distances, even marginal estimates of density based on mark and recapture methods may be impossible to obtain. In the sidewinder study at Kelso, 53 sidewinders were marked over the 2-year period. Of these, only six were recaptured and only two were recaptured more than 5 days after being released.

Tracking Snakes in Chaparral

Tracking offers a promising approach for ecological studies in a variety of habitats where vegetation density and climate are not major constraints. Tracking is possible on a variety of fine-textured soils, and even coarse or hardened surfaces can be modified for tracking purposes. In areas of moderately dense vegetation, tracks can be sampled from strips or patches of cleared substrate. For example, snakes have been studied in Quebec using fine sand transects constructed in woods and fields, protected from rain by a canopy (Bider 1968).

Since 1971, effort has been directed toward comparing the abundance of active snakes in burned and unburned patches of chaparral in San Diego County, California. This study is still in progress, and the purpose here is not to report conclusions but to suggest directions; throughout the study I have attempted to identify situations in which tracking might offer practical advantages as a field method in herpetological investigations.

Sampling Techniques

The use of tracks to quantify the activity and relative abundance of snakes was stimulated initially by the hypothesis (corroborated by cursory field observations) that snake populations were reduced in burned habitat either as a direct or indirect consequence of fire. Snakes are not easily observed, and, especially under conditions of low population density (or activity), the "catchability" of specimens diminishes significantly. However, sampling is

Fig. 2. A road bearing excellent tracking surface in remote chaparral (San Diego County, California).

always possible by tracking; if any number of snakes are active, their tracks will be evident.

I have used dirt roads as transects for sampling tracks in chaparral habitats. Distances exceeding 2 km in each of burned, unburned, or ecotone chaparral were censused two or three times daily for variable periods during seasons of peak snake activity (May–July). Each transect was traversed in both directions during a given census to allow optimal visibility of tracks, which depends on the direction of oblique lighting, particularly when the sun is low. Tests demonstrated that even the smaller snakes of the area (e.g., juvenile *Hypsiglena torquata*) left detailed impressions when crawling upon the surfaces of dirt roads that were used in the study. Information about the size, species, and direction of a snake's travel was easily obtained from inspecting tracks that were found on the transects. Counts of tracks can potentially be used to quantify the relative abundance and species densities of active snakes and can provide detailed information about the spatial and temporal aspects of activity. Moreover, different areas can be sampled simultaneously, thus enabling one to investigate the geographic synchrony of activity patterns.

Dirt roads traverse remote areas of chaparral in California and permit extensive sampling of habitat (Fig. 2). Many of these roads are adequate for tracking except in areas having very coarse soils or where motor vehicle traffic is excessive. Some motor vehicle traffic is actually desirable because it creates and maintains a fine-textured substrate. Even where the investigator elects not to use tracking as a principal method of study, much preliminary information regarding abundance, species composition, etc. might be obtained in a short period from track counts on roads.

In a study of snake movements in eastern Kansas (Fitch and Shirer 1971), it was shown that snakes sometimes avoided crossing roads. This appears not to be a problem in chaparral where the vegetation forms a much less continuous ground cover (at substrate level) than in the more mesic habitats of eastern Kansas. In chaparral, the number of tracks on dirt roads compared favorably with the number of tracks occurring on narrow (1 m) strips of tracking substrate in off-road habitats where natural breaks in vegetation equalled or exceeded the width of the tracking substrate. Moreover, out of hundreds of observations of tracks in chaparral, the number of occasions where a track indicated that a snake approached or entered upon a road and then reversed its direction was extremely rare (< 1% of observations). I have observed several situations in which snakes crossed dirt roads repeatedly during day-to-day wanderings within a specific home range.

In addition to roads, tracking surfaces can be prepared *in situ* wherever there is sufficient exposed soil. Brushing or scraping the ground with a heavy pushbroom creates suitable substrate by removing large debris and abrading coarse surfaces. These "scrubbing" procedures have been used to create strips and grids of trackway in several areas of chaparral (Fig. 3). The "grids" of trackway were not arrayed in a regular geometry. Tracking surfaces comprising a grid followed the natural openings between shrubs and rock (usually a few meters apart) and were spaced so that movements of any snake within a unit area of habitat could be detected.

In this manner I have monitored the occurrence of tracks on 0.5-ha grids for relatively short periods (one to several weeks). Although it was not possible to enumerate snake densities on these sites owing to the limited time and area sampled, the observations did demonstrate the feasibility of relating tracks to habitat area, even in relatively dense brush. I was able to follow the movements of individual snakes on these grids, and I was able to identify and even capture them. More intensive efforts at tracking a larger area would enable an investigator to quantify the numbers (but see below), kinds, and activity of snakes in a given patch of habitat.

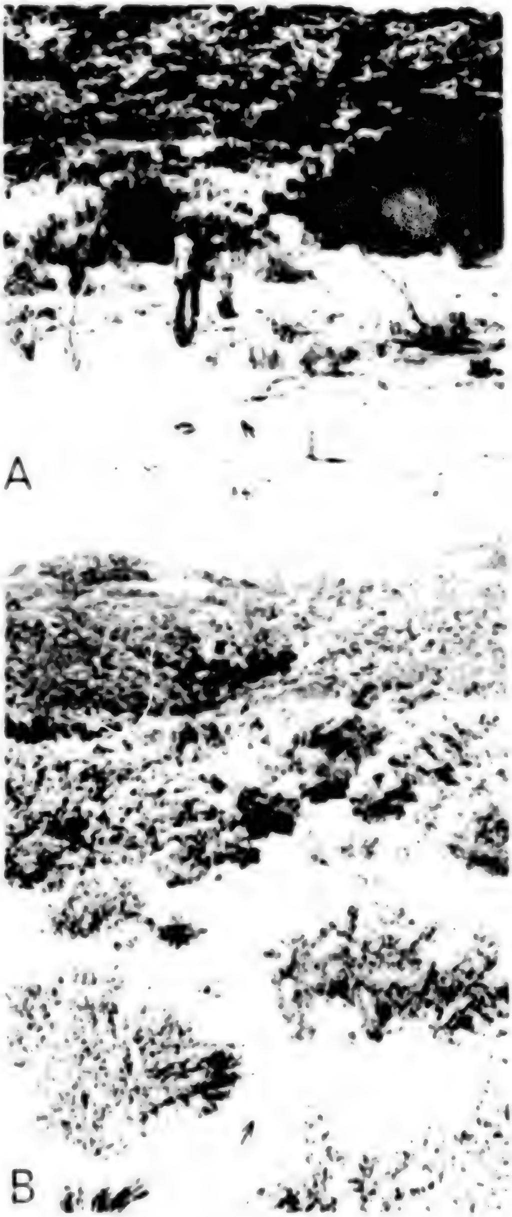

Fig. 3. Tracking strips (arrows) created by scraping and brushing topsoil in (A) recently burned chaparral and (B) chaparral 15 years or older.

Identifying Snakes from Their Tracks

In chaparral, snake tracks have distinct characteristics, and the trained observer can distinguish these from other marks or impressions that tend to resemble those of snakes. If a dirt tracking surface has a sufficiently fine texture, a fresh snake track (age < 18 h) appears reflective or lustrous, especially when viewed obliquely. This quality is attributable to the compression of substrate particles by the snake's weight during efforts at locomotion. Lizard tracks usually can be distin guished by the presence of foot impressions and the low reflectance quality (lack of sheen or luster) of the tail drag (Fig. 4A). However, the foot impressions may be obscured or even absent in certain circumstances. Tracks of the lizard *Gerrhonotus* spp. (and probably large scincids in other habitats) are an exception to this generalization, as the body and the tail produce a lustrous track. In these cases, however, impressions of feet and even digits are usually well preserved. Ant trails may superficially resemble snake tracks, but the dirt lacks compression and the high reflectance (luster).

It is widely known that tracks of vipers which sidewind on desert dunes are easily recognized owing to their unique mode of locomotion. It is also possible to identify tracks which are produced by snakes having less unique and even similar locomotory modes. In the chaparral near Mount Laguna, San Diego County, California, I have been able to identify tracks made by rattlesnakes (*Crotalus viridis*), gopher snakes (*Pituophis melanoleucus*), and striped racers (*Masticophis lateralis*). An account follows of the criteria by which the tracks of these three species might be distinguished.

Pituophis melanoleucus (Fig. 4B). This snake typically progresses in a rectilinear or concertina mode (for terminology, see Gans 1970). Consequently, the tracks of this snake are quite straight but sometimes exhibit abrupt curvatures where force transmission is directed backward. The body presses firmly against the substrate, and the tracks of this snake are normally continuous throughout their length.

Crotalus viridis (Fig. 4C and D). The tracks of this snake are readily distinguished from those of sympatric non-crotalid species. Identifying features are attributable to the weight of these snakes and their habit of carrying the rattle erect. The track may be straight or sinuous but is almost always unbroken, and the soil is pressed firmly. The track is often deep and typically appears as though several snakes had traversed the same region of substrate. This effect seems to be caused by the sliding of the body as the snake attempts to gain traction during effective undulating. The trailing end of the snake is broad and blunt owing to the erect position of the rattle, and the tail at the base of the rattle forms a broad depression within the width of the main track. "Tail drags" are also seen in tracks of other snakes, but only in rattlesnakes are they relatively broad in relation to the width of the entire track.

Masticophis lateralis (Fig. 4E and F). The track of this species is distinguished from the previous two because it undulates broadly and is usually discontinuous. Ridges and depressions formed at points of force transmission are deep and sharply defined, and tail drags often cross the main track obliquely.

Snakes can sometimes be found by searching in the immediate vicinity of freshly-made tracks, particularly if searches are conducted along dirt roads during peak hours of snake activity. I have used this collecting procedure to affirm empirically my ability to identify tracks of rattlesnakes, gopher snakes, and striped racers. Snakes were identified correctly in 100% of 30 accumulated cases where track identifications were subsequently verified by capturing the snake. Clearly, more data are needed to establish the reliability of track identification, but the method at least appears promising. The three species of snake mentioned here include the more common or conspicuous snakes in the Mount Laguna chaparral and account for 90% of all snakes that were seen or collected during a 3-year period. It may be possible to identify the tracks of at least some of the other snakes present in chaparral, but I have had limited opportunity to observe them.

In cases where identifications are uncertain, tracks might be assigned to species on the basis of probability values. For example, two species of rattlesnake can be found in the Mount Laguna area: *C. viridis* and *C. mitchelli*. The latter species is relatively uncommon in certain areas, and in the locality where my studies were conducted, it accounted for only 2 out of 48 rattlesnake sightings during a 3-year period. In this example, it seems reasonably secure to assume that something in excess of 90% of *Crotalus* tracks result from the activity of *C. viridis* (assuming that tracks of *C. viridis* and *C. mitchelli* are indistinguishable). Intensive sampling would presumably allow one to develop a more rigorous quantitative basis for assigning to species tracks that are potentially ambiguous. Further research on the species specificity of track characters seems potentially valuable at this time.

An alternative procedure is to assign "ambiguous" tracks to ecological guilds of snakes rather than to species. Rattlesnakes and racers are

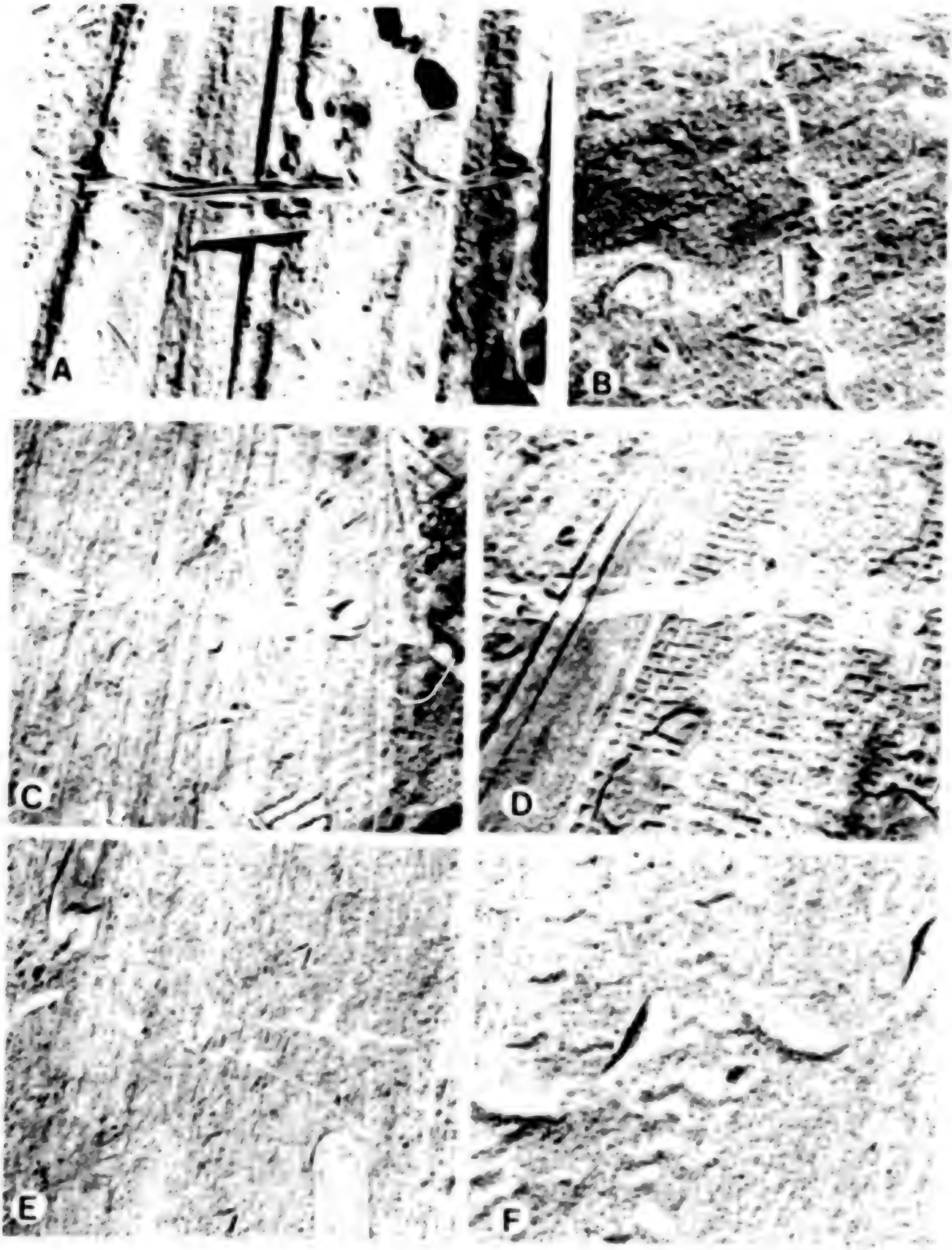

Fig. 4. (A) Lizard tracks (probably *Cnemidophorus tigris* and *Uta stansburiana*) illustrating foot impressions and low reflectance quality due to the "drag" of the tail. (B) Track of adult *Pituophis melanoleucus* illustrating the effects of concertina as well as rectilinear locomotion. (C and D) Tracks of adult *Crotalus viridis* (note tail impressions within the main track). (E and F) Tracks of adult *Masticophis lateralis*. Note the discontinuity of the track, sharp ridges, and oblique tail drags (arrows).

examples of two possible categories. This level of resolution might be adequate for certain kinds of ecological investigations.

Although in small mammal tracking it is possible to recognize individuals which have been toe-clipped or banded, the possibility of recognizing large numbers of tagged snakes from individual tracks is unlikely. However, it is possible to recognize the tracks of a small number of individually tagged snakes from drag marks produced by metal bands which are attached to a posterior scute (unpublished observations); such identifications could be useful in limited circumstances. Snakes may frequent a specific area, at least during certain periods, and will often move in regular circuits within a "home range" of habitat. Thus, a localized, repeated spatial pattern of identically shaped tracks probably denotes a particular individual. I have confirmed this by repeatedly capturing scale-clipped snakes which were identified and subsequently relocated by tracking. Such snakes conceivably could be tagged once for individual track recognition and then followed without further disturbance. Individual tagging could also be useful in distinguishing the tracks of a limited number of resident animals from those left by "transients" on a particular plot. Several snakes could possibly be recognized individually by varying the width or number of bands attached to scutes.

Social Behavior

Documented aspects of the social behavior of snakes usually are related to reproduction, aggression, or denning activities. There is limited information on whether snakes move in social groups during the active season, but such behavior conceivably could be learned from tracks. Numerous and systematic observations of tracks in chaparral indicate that snakes occasionally move in pairs. When crossing roads, snakes usually leave a track which is more or less perpendicular to the length of the road and which is not associated with other impressions. Occasionally, two (and rarely three) tracks occur together and have topographies indicating that one snake had crawled almost directly over the track of another. I interpret these tracks to indicate purposeful social behavior, possibly related to sexual pairing and mediated by chemical (pheromone) communication. On one occasion, search for the snakes associated with such a "double track" revealed two adult *C. viridis*, a male and a female, lying together in a loose coil beneath a shrub. These snakes were perfectly immobile and not engaged in any overt sexual activity. The snakes were observed for about 15 min and then disturbed for the purpose of making positive sex identifications (by probing the tail with a blunt instrument). In another instance, two adult *M. lateralis* were observed only a few meters apart when I followed a "double track" offroad into an area of grass and oak trees. Only one of the snakes was captured.

Double tracks were found during spring and summer, suggesting that pair associations might not be limited to periods of courtship and copulation. Other observations indicate that the same individual snake will crawl repeatedly over the exact same route. In view of these findings, studies of pheromone trailing behavior in snakes, now well documented in the laboratory (Gehlbach et al. 1971; Ford 1975; Kubie and Halpern 1975), might profitably be extended to natural situations.

One other observation is noteworthy. In the late morning of 26 July 1973, eight tracks appeared on a short distance of road (approx. 5 m) within a brief period (believed to be less than 1 h and probably no longer than a few minutes). All of these tracks were identical in size and topography, and they all indicated a common direction of movement away from a grassy meadow toward a tree-covered hillside. Searching the nearby hillside eventually produced one adult *Coluber constrictor*, but no other snakes were found. Two of the eight tracks were made during the few minutes while searching efforts were in progress, and four of the other tracks occurred in pairs (two sets of double tracks). The identical appearance of these tracks suggested that all of the snakes were about the same size and probably belonged to the same species, while their temporal and spatial occurrence suggested that there was group structure to the movements of these eight individuals.

The recent discussion of social behavior in juvenile green iguanas by Burghardt et al. (1977) focuses attention on complex social patterns in reptilian groups. Interest in this subject might profitably be extended to snakes, as indicated by accounts of denning activities (e.g., Woodbury et al. 1951; Klauber 1956), communal egg laying (Brodie et al. 1969; Gregory 1974, Palmer and Braswell 1976), and unexplained non-wintering aggregations (e.g., Kropach 1971). From the tracking observations, it may be inferred that a significant amount of snake movements has social structure. With rigorous tracking efforts, it should be possible to follow through time the social interactions between known individual snakes residing on tracking grids in natural environments.

The Dynamics of Snake Populations

Almost all present knowledge concerning the population ecology of snakes has been generated by capture–recapture analysis. Turner (1977) recently evaluated density estimates for snakes and concluded that the reliability of these measures is questionable in almost all cases. What seems to receive little attention is the blunt fact that even the best estimates relate only numbers of surface-active snakes to a specific area at a particular time. We do not know how accurately these estimates reflect absolute density (considering the environment in three dimensions) or whether the numbers of individual snakes registered comprise a natural demographic unit. In areas of low population size (or activity), density estimates based on capture–recapture methods have unacceptably large variances, and problems related to the "catchability" of snakes frequently invalidate the assumptions which underlie the analysis.

There are no easy solutions to these problems. However, in appropriate habitats tracking might improve our capacity to capture individual snakes and reveal more directly the temporal variability of activity. Tracks might also assist in determining whether snakes belonging to a particular species or locality are widely dispersing (e.g., *C. cerastes*) or are structured demographically into more localized units. Tracking techniques would be of tremendous value in attempts to enumerate densities of snakes by their removal.

Some of the sampling problems in relation to density estimates are suggested by reference to Fig. 5, which depicts counts of snake tracks determined in two successive years at the same locality near Mount Laguna. The number of tracks that were evident in 1973 greatly exceeded those of the previous year (e.g., there was nearly an eight-fold increment of tracks which were 1.0 to 1.5 cm in width). Size classes of tracks were arbitrarily delimited and reflect measurements of average width. Generally, hatchling or yearling snakes produce tracks smaller than 1 cm wide. The data in Fig. 5 indicate that the increment of snake activity observed in 1973 cannot be attributed to a recruitment of young born the previous year. Changes in the number of tracks must reflect either changes in the number of active snakes or changes in the activity of individual snakes, or both. Observations of the characteristics of tracks in relation to their temporal and spatial occurrences indicated that the differences in numbers of tracks reflected, at least in part, changes in the number of active snakes.

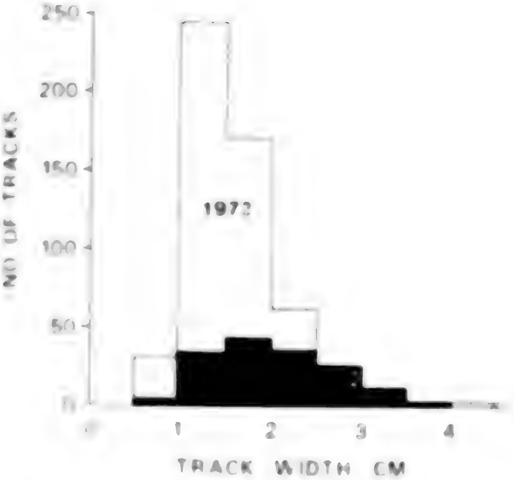

Fig. 5. Counts of snake tracks from 2 km of dirt road [illegible] days within the period 15 June to 15 July [illegible]

How can we account for the differences in snake behavior observed during these two years? In 1972 precipitation was far below normal and conditions were much drier than in 1973 (winter precipitation in 1972–73 exceeded that in 1971–72 by more than fourfold; Keeley 1977). Whether habitat aridity produced the observed changes in snake activity between 1972 and 1973 cannot be concluded unequivocally, but the correlation is compelling. The relationship between increased precipitation and increased snake abundance has been noted elsewhere (e.g., Conant 1938, Fitch 1965, Clark 1970). It can be hypothesized that dry conditions suppress activity in "dry" years or that excessively moist conditions stimulate activity in "wet" years, or both.

An important implication of these data is that changing climatic conditions may cause snakes to spend much (perhaps all) of the active season in seclusion where they are inaccessible to capture or observation. If this is so, changes in the densities of snake populations reported over time (e.g., Klimstra 1958; Fitch 1965; Clark 1970; Prestt 1971; Parker and Brown 1973) may merely reflect changes in activity (behavioral density). It is inaccurate to refer to such phenomena in terms of absolute densities unless the spatial or activity limitations are specified. Clearly, many species of snakes might conduct feeding and other essential activities within spatial dimensions of habitat inaccessible to the human observer, and this could also account partially or wholly for the reported "rarity" of certain species. Energy budgets of ectothermic vertebrates permit prolonged periods of dormancy; periods in which aboveground activity is negligible or absent are known to exceed a full year in amphibians (Mayhew 1965) and in lizards (Turner et al. 1969). The above discussion emphasizes the difficulty of studying the comparative demography of snakes.

Another interesting feature of the data in Fig. 5 is the small proportion of tracks that includes yearling snakes (tracks 0.5 to 1.0 cm wide). The inferred low activity of snakes in this size class, at least in certain seasons, possibly accounts for the more general observation that younger-aged snakes are under-represented in collections from live traps (Fitch 1963*a*, 1963*b*; personal communication; Hirth and King 1968). For this reason alone, many estimates of the age structure as well as density of snake populations are likely to be inaccurate. The diminished activity of younger snakes, relative to adults, may be related to avoidance of exposure to higher rates of predation, avoidance of higher rates of evaporative water loss due to less favorable surface-mass ratios, and possibly frequent feeding to maximize growth (snakes digesting food tend to be inactive). Dispersal in snake communities thus may be accomplished by older rather than (or in addition to) younger individuals, as is suggested in Brown's study (1970) of sidewinders.

In summary, I share completely Turner's (1977) skepticism about our present capacity to estimate population densities of snakes. While it appears feasible to relate numbers of active snakes to both time and spatial dimensions of habitat, there is great difficulty in determining qualitatively and quantitatively the proportion and elements of the total population structure which have actually been sampled. Hopefully, these deficiencies can be improved with the application of intensive and more sophisticated effort in ecological research. Particular attention should be paid to the subterranean ecology of snakes. In aboveground studies, tracking can improve sampling and provide detailed resolution of activity patterns in terrestrial communities.

Acknowledgments

This paper is dedicated to the memory of Timothy Brown. I express my sincerest appreciation to the students who have assisted me in various phases of the field studies in chaparral. I am also grateful to H. Fitch and W. Duellman who commented on the manuscript.

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Field Techniques for Herpetofaunal Community Analysis

by

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Abstract

A standardized amphibian and reptile trapping system is described and compared with other survey techniques. The new sampling system has proven very effective for sampling small, secretive, terrestrial species, but must be used in conjunction with other more conventional techniques to obtain a complete herpetofaunal species list.

Over the past several years we have had the opportunity to undertake several intensive herpetological sampling programs and to employ and evaluate a variety of sampling techniques in different habitat types in Florida. In the course of these studies we have developed and standardized a trapping system that we believe can be employed in many terrestrial habitats. The data obtained from this technique allow estimates of species richness and provide an index of the relative abundance of most common terrestrial amphibian and reptile species. The technique by itself, however, does not reliably sample all species in a habitat and must therefore be coupled with specific search techniques for those species less likely to be taken in the trapping system. The combination of our trapping method and the appropriate specific search technique will, however, provide a maximum amount of information on the amphibians and reptiles in any specific region with a minimum amount of effort. Here we describe our array system and compare it with other herpetofaunal sampling techniques. A similar system has been developed independently by Vogt and Hine (this volume).

Array System

Our sampling array is a system of pitfall and double-ended funnel traps placed in conjunction with drift fences which divert moving animals into the traps (Fig. 1). The drift fences are 7.6-m lengths of 46-cm-high "valley tin" arranged in a plus-shaped pattern with a central separation of 15 m. Each arm has a 19-L plastic paint bucket sunk flush with the ground at each end. The tin fence overhangs the bucket slightly and fits into a slot cut into the plastic bucket. A masonite board raised 2 to 4 cm above the lip of the bucket provides shade and keeps rain and litter out. In most soil types (including loose sand) support stakes are not needed; simply burying the fence about 10 cm into the ground keeps it firmly upright.

The funnel traps are constructed of 76-cm aluminum window screening rolled into a cylinder about 20 cm in diameter. Funnels are fashioned out of 38- × 38-cm screening and inserted into each end of the cylinder. The whole trap is assembled with ordinary office staples. Specimens can be removed with forceps or tongs through either end. The funnel traps are placed flush with the ground and appressed to the tin fence, one on each side of each arm. Loose soil or ground litter is brushed into the mouth of the traps to create a more natural entry. A masonite board is placed against the fence over the trap to provide shade.

A team of three field persons can, with a little practice, install a complete array in 1–2 h, depending on the habitat. The four drift fence arms are staked out at right angles to each other

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[1] Deceased: Died at Gainesville, Florida, on 10 December 1981.

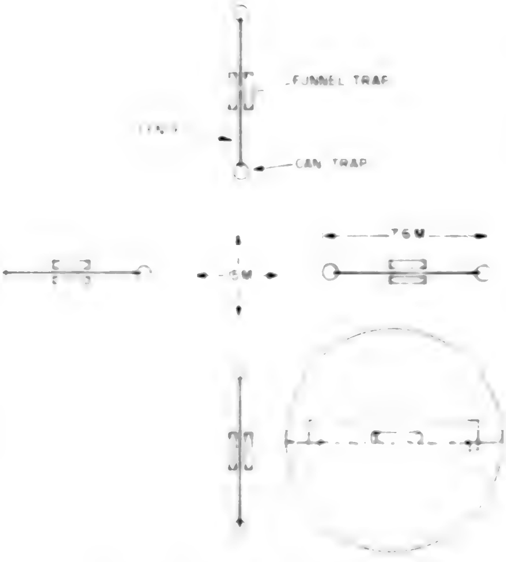

Fig. 1. Standard amphibian and reptile sampling array system

and a trench is dug for each arm. The bucket holes are then dug on each end of the trench and the buckets installed. As two people hold the fence up in the trench, a third person fills the soil back in, packing it down as he proceeds, using alternate downward pressure from the right and left foot.

After 22 months, 20 arrays in the Ocala National Forest, Florida, are still operating and have required virtually no maintenance. The buckets and fences do not rust and the pressure-treated masonite is not damaged by insects. The total cost of materials is about $65 for each array.

Because the arms of an array are at right angles to each other, no directional bias is introduced by its placement. Thus arrays can be constructed at random locations without regard to natural animal migration routes and yet still intercept moving animals coming from any direction. Our standard procedure is to install two arrays a minimum of 100 m apart in a habitat type. The traps are checked once a week, and although the shrews and mice are usually dead, the arthropods, amphibians, and reptiles are generally in good condition and can be marked and released or saved as desired.

During the Cross Florida Barge Canal Wildlife Restudy (Florida Game and Fresh Water Fish Commission 1976), we operated 30 arrays for a total of 7,432 array-days in 11 different habitat types. These traps collected 1,644 specimens of 43 species of amphibians and reptiles for an average of 0.22 specimen per array-day, or 1.55 specimens per array each time they were checked (Table 1). The relative effectiveness of the funnels versus the buckets in an example site can be seen in Fig. 2.

These data are of considerable importance in comparing faunal associations in a study area. The can-trapping technique has inherent biases for certain types of animals. Species that are agile climbers (e.g., treefrogs [Hylidae]) may escape from the traps and are seldom taken. Similarly, large snakes may enter and leave the can traps at will; however, large snakes and occasionally treefrogs are taken in the funnel traps. Masonite can covers generally exclude turtles with the exception of an occasional small specimen. Overall, the arrays tend to select for the smaller surface-active amphibians and reptiles as well as terrestrial arthropods and shrews and rodents. One species, the introduced greenhouse frog (***Eleutherodactylus planirostris***), appeared to have a positive orientation to the cans as refuges and congregated in them in large numbers even though capable of climbing out at will. Can traps are unsuitable for use in habitats where the soil is fully saturated or for use below the ground water level. However, in these sites we replace the buckets with larger diameter funnel traps made of window screening, which our preliminary results suggest are almost as effective as the buckets.

The data collected by the array system can be used in a variety of ways to characterize and compare habitats. Besides generating species lists, arrays provide a clear indication of relative abundances between habitat types (Fig. 3). Species diversity indices can be calculated for the samples, and species richness and abundances can be compared across habitat types (Table 1). Seasonal patterns in surface activity may become readily apparent (Fig. 4). The specimens collected can be used to estimate reproductive patterns, growth rates, age-class representation, biomass relations, food habits, and infraspecific variability.

Other Can-trapping Methods

During the study, we also tested several other types of pitfall trapping systems. All were set within 500 m of the standard arrays in the same

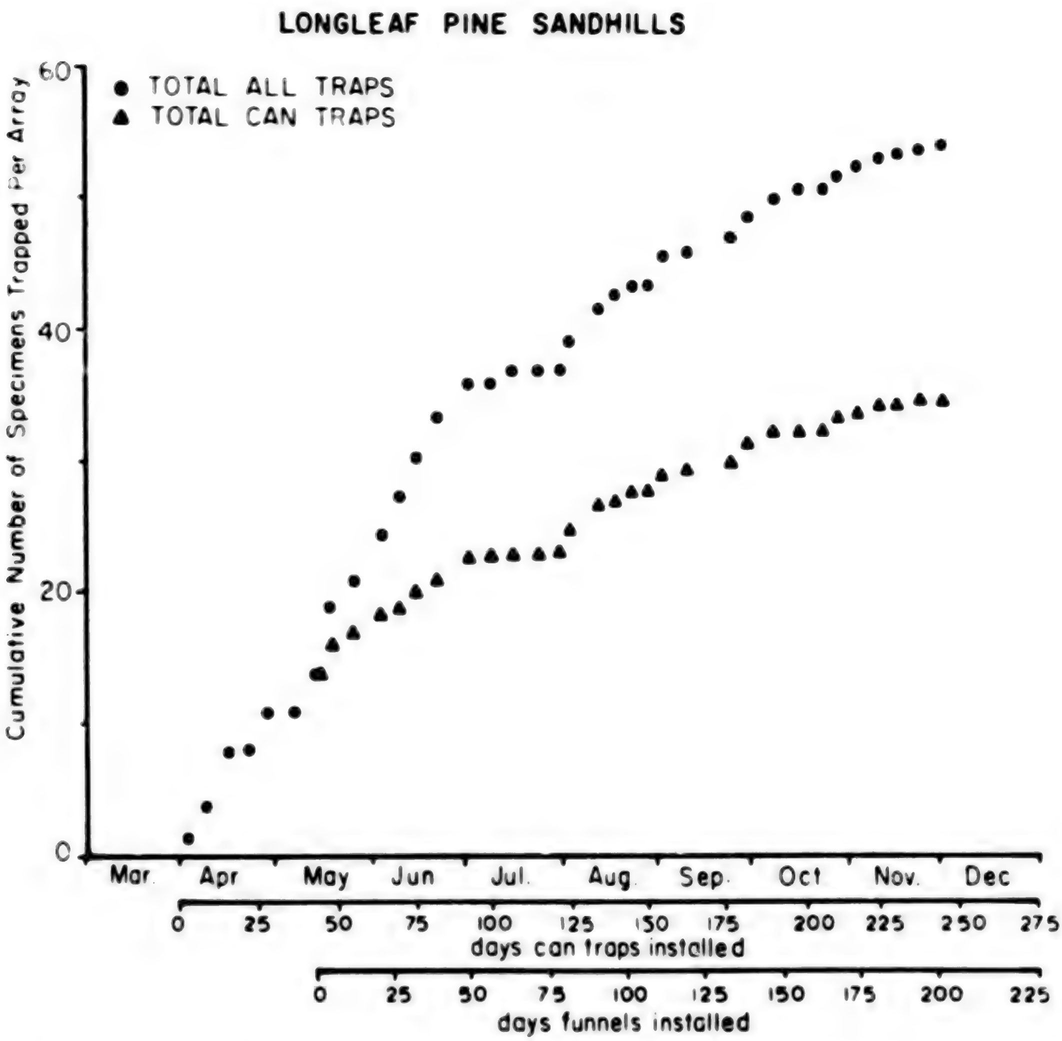

Fig. 2. Relative effectiveness of funnel traps versus can traps in longleaf pine sandhills, Florida

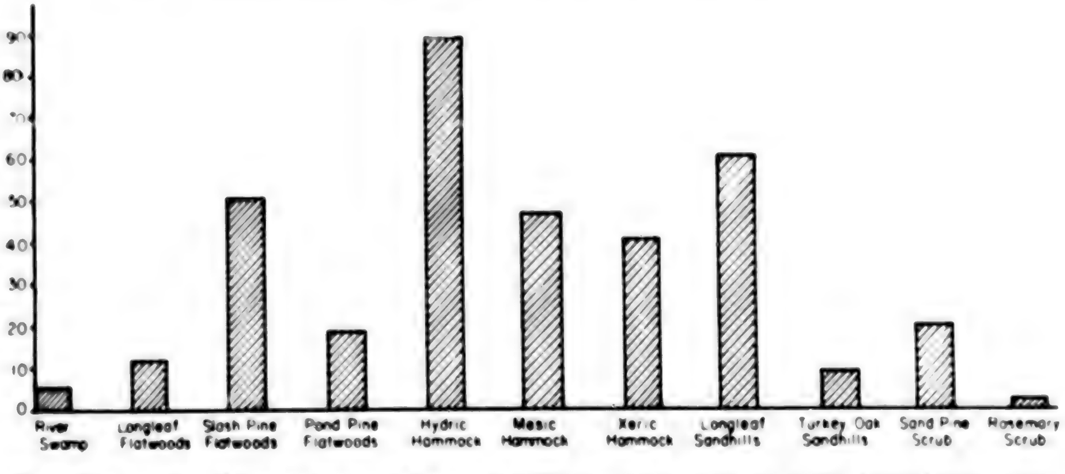

Fig. 3. Total number of *Gastrophryne carolinensis* (× 1,000) trapped per array-day by the standard array system during the Cross Florida Barge Canal Wildlife Restudy in 11 different habitat types.

Table 1. *Total numbers and adjusted relative values (individuals per array per day × 1,000) of amphibians and reptiles trapped in 30 arrays in 11 sites along the route of the proposed Cross Florida Barge Canal (Florida Game and Fresh Water Fish Commission 1976).*

Species	River swamp	Longleaf flatwoods	Slash flatwoods	Pond pine flatwoods	Hydric hammock	Mesic hammock	Xeric hammock	Longleaf sandhills	Turkey oak sandhills	Sand pine scrub	Rosemary scrub	Total all sites
Eleutherodactylus planirostris		151(163.4)	89(305.8)	–	–	438(944.0)	–	–	1(0.9)	–	–	679(91.2)
Kinosternon bauri		–	–	–	1(1.9)	–	–	–	–	1(0.9)	–	2(0.3)
Rhineura floridana		–	–	–	–	–	–	–	–	1(0.9)	1(1.8)	2(0.3)
Anolis carolinensis		1(1.1)	–	–	7(13.4)	9(19.4)	10(25.6)	4(5.4)	5(4.6)	6(5.6)	3(5.5)	45(6.0)
Sceloporus undulatus	–	3(3.2)	–	–	–	–	–	–	9(8.2)	–	1(1.8)	13(1.8)
S. woodi		–	–	–	–	–	–	–	–	1(0.9)	–	1(0.1)
Cnemidophorus sexlineatus		–	–	–	–	–	–	9(12.2)	3(2.7)	3(2.8)	19(34.8)	34(4.6)
Ophisaurus ventralis	–	–	–	–	–	–	–	–	1(0.9)	–	–	1(0.1)
Eumeces egregius		–	–	–	–	–	–	–	14(12.8)	3(2.8)	14(25.6)	31(4.2)
E. inexpectatus		14(15.2)	–	1(6.0)	–	–	2(5.1)	19(25.7)	16(14.6)	28(26.0)	10(18.3)	90(12.1)
E. laticeps		–	1(3.4)	–	1(1.9)	–	4(10.3)	–	–	–	–	6(0.8)
Scincella laterale		27(29.2)	2(6.9)	3(18.1)	20(38.2)	16(34.5)	3(7.7)	38(51.5)	31(28.3)	18(16.7)	1(1.8)	159(21.4)
Cemophora coccinea					–	–	–	–	–	4(3.7)	3(5.5)	7(0.9)
Coluber constrictor					–	–	–	–	–	1(0.9)	2(3.7)	3(0.4)
Diadophis punctatus			1(3.4)	–	3(5.7)	–		–	–	1(0.9)	–	5(0.7)
Heterodon simus					–	–	–	–	2(1.8)	–	–	2(0.3)
Masticophis flagellum	–	–			3(5.7)	–		–	1(0.9)	–	1(1.8)	5(0.7)
Pituophis melanoleucus		–			–	–	–	1(1.4)	–	–	–	1(0.1)
Storeria occipitomaculata	–				1(1.9)	–	1(2.6)	–	–	–	1(1.8)	3(0.4)
Notophthalmus perstriatus		1(1.1)	–		–	1(2.2)	–	–	–	–	–	2(0.3)
Plethodon glutinosus		–	–	–	3(5.7)	–	–	–	–	–	–	3(0.4)
Scaphiopus holbrooki	–	17(18.4)	–	2(12.0)	18(34.4)	17(36.6)	8(20.5)	5(6.8)	1(0.9)	3(2.8)	2(3.7)	73(9.8)
Gastrophryne carolinensis	1(6.9)	12(13.0)	15(51.5)	3(18.1)	47(89.7)	22(47.4)	16(41.0)	45(61.0)	10(9.1)	22(20.4)	2(3.7)	195(26.2)
Bufo quercicus	–	2(2.2)	–	17(102.4)	–	–	–	–	–	1(0.9)	1(1.8)	21(2.8)
B. terrestris	3(20.8)	28(30.3)	1(3.4)	3(18.1)	5(9.5)	13(28.0)	8(20.5)	6(8.1)	6(5.5)	32(29.7)	10(18.3)	115(15.5)
Acris gryllus	–	–	–	–	–	–	–	1(1.4)	–	–	–	1(0.1)
Hyla cinerea	–	–	–	–	–	1(2.2)	–	–	–	–	–	1(0.1)
H. crucifer	–	–	–	–	1(1.9)	–	–	–	–	–	–	1(0.1)
H. femoralis		2(2.2)	–	–	–	1(2.2)	–	–	–	–		3(0.4)
H. gratiosa		–	–	–	–	–	–	–	–	1(0.9)	–	1(0.1)
H. squirella	–	2(2.2)	–	–	–	–	–	–	–	–	–	2(0.3)
Limnaoedus ocularis		4(4.3)	–	–	1(1.9)	–	–	–	–	–	–	5(0.7)
Rana areolata	–	–	–	–	–	–	–	–	–	–	1(1.8)	1(0.1)

Table 1. Continued

Species	River swamp	Longleaf flatwoods	Slash flatwoods	Pond pine flatwoods	Hydric hammock	Mesic hammock	Xeric hammock	Longleaf sandhills	Turkey oak sandhills	Sand pine scrub	Rosemary scrub	Total all sites
R. catesbeiana						2(4.3)	—		—	—	—	2(0.3)
R. clamitans			—		2(3.8)		2(5.1)		—	—	—	4(0.5)
R. grylio						1(2.2)			—	—	1(1.8)	2(0.3)
R. heckscheri	3(20.8)								—	—	—	3(0.4)
R. sphenocephala		2(2.2)		—	4(7.6)	16(34.5)	—		—	—	2(3.7)	24(3.2)
Stilosoma extenuatum			—		—		—		1(0.9)	—	1(1.8)	2(0.3)
Tantilla relicta				—			5(13.0)	27(36.6)	17(15.5)	20(18.6)	11(20.1)	80(10.7)
Thamnophis sirtalis		1(1.1)	1(3.4)	—	2(3.8)			3(4.1)	—	—	—	7(0.9)
Sistrurus miliarius				—	1(1.9)		—	2(2.7)	1(0.9)	—	—	4(0.5)
Micrurus fulvius						—		2(2.7)	—	1(0.9)	—	3(0.4)
Total Species	3	16	7	6	17	12	10	13	16	19	21	43
Total Individuals[a]	7(48.6)	116(125.5)	21(72.2)	29(174.7)	120(229.0)	99(213.3)	79(151.3)	162(219.5)	118(107.7)	147(136.5)	87(159.3)	965(129.8)
Shannon-Wiener Index[a]	1.00	2.10	1.04	1.32	2.01	1.98	2.04	1.97	2.21	2.22	2.46	2.61

[a] *Eleutherodactylus* has been omitted from these calculations. See text

habitats. Two arrays were constructed without drift fences and funnel traps, but were otherwise identical to the standard. These were ineffective, taking only an occasional specimen of *Sceloporus undulatus* and *Cnemidophorus sexlineatus*.

In another experiment we set up a continuous 30-m tarpaper drift fence with eight buckets and eight funnel traps, representing the same length and number of traps as a standard array. This system proved only marginally effective, primarily because the tarpaper fence had a tendency to droop in the summer heat and required almost daily maintenance.

We also installed six sets of 3-m-long pressure-treated boards with a jar-funnel trap on each end as described by Clark (1966). Although these traps proved effective for Clark in Kansas, they collected only a single specimen of *Gastrophryne* in Ocala. The 3-m board may not be a long enough fence to interrupt animal movements in the open Florida sandhills and scrub habitats, and their low (12- to 14-cm) height may not effectively divert some species.

Quadrat Method

Sampling amphibians and reptiles by attempting to collect all individuals in a specified quadrat has been used in previous herpetofaunal surveys (e.g., Lloyd et al. 1968; Heyer and Berven 1973; Scott 1976 and this volume; Inger and Colwell 1977). We tested this technique during the study at four of the same sites where our herp arrays were already operating, but at a minimum of 500 m away from the arrays. Three replicates were performed in each habitat type, one each in the spring, summer, and autumn. Quadrats of 1,000 m² were marked off with nylon string and searched by a team of three or four experienced field herpetologists. Larger and more active species were noted as they dispersed off the quadrat. Several passes were then made through the marked area removing surface litter and inspecting all possible retreats. An average of 6 man-hours was required to reach the point where we felt additional collecting would yield no more specimens.

Time-constrained Technique

We used the same four sites to test the method

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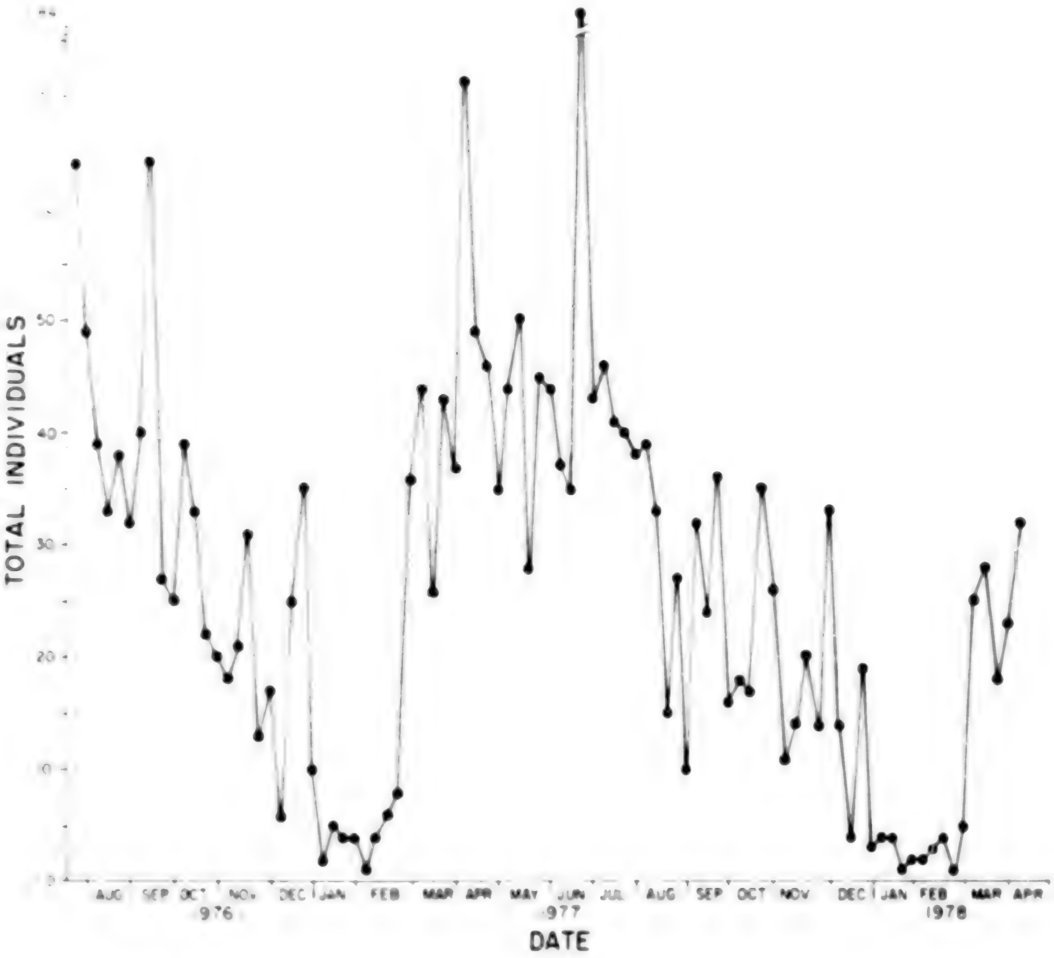

Fig. 4. Total individuals trapped by date at six sites (12 arrays) in sand pine scrub in the Ocala National Forest, Florida. Trapping effort was equal at each site

of general herpetological collecting per unit time. There were no boundaries except that the collectors remained inside the specific habitat and at least 500 m away from the arrays and 1,000-m² quadrats. Experienced field herpetologists moved through the habitat turning logs, inspecting retreats, and watching for surface-active amphibians and reptiles. Three 6-man-hour replicates were performed in each habitat type, one each in the spring, summer, and autumn

Comparison of Quantitative Techniques

Inspection of Table 2 shows that in the sandhill and scrub habitats, the array system yielded the maximum returns for approximately equal effort expended. Both of these habitat types are dominated by pine trees which offer little cover for amphibians and reptiles. However, in the flatwoods and hammocks, cabbage palm (*Sabal palmetto*) and several broadleafed scrubs and trees provide hiding places for treefrogs that are not usually collected by the arrays. Small wet areas in both flatwoods and hammock sites provide additional microhabitat for species not normally encountered in the drier sandhills and scrub.

Nocturnal Road Cruising

Road cruising or night driving is a well-known technique involving driving a vehicle at

Table 2. *Total numbers of individuals and species collected at four sites (slash pine flatwoods, xeric hammock, turkey oak sandhills, and sand pine scrub) along the route of the proposed Cross Florida Barge Canal by three sampling techniques.*

	Quadrat		Time-constrained		Array	
Habitat type	No.	Species	No.	Species	No.	Species
Slash pine flatwoods	30	9	31	14	110	7
Xeric hammock	39	6	106	18	59	10
Turkey oak sandhills	30	6	75	13	119	16
Sand pine scrub	23	8	48	10	148	19
Total	122	15	260	24	436	29

Table 3. *Amphibian and reptile species collected during the Cross Florida Barge Canal Wildlife Restudy by three sampling techniques at four sites (slash pine flatwoods, xeric hammock, turkey oak sandhills, and sand pine scrub) and by nocturnal road cruising through a wider variety of habitats. R = road cruising, Q = quadrats, TC = time-constrained, A = array system*

Species	R	Q	TC	A
Notophthalmus viridescens			x	
Plethodon glutinosus			x	
Scaphiopus holbrooki	x			x
Gastrophryne carolinensis	x	x	x	x
Bufo quercicus	x			x
B. terrestris	x	x	x	x
Acris gryllus				
Hyla chrysoscelis	x			
H. cinerea	x		x	
H. crucifer	x	x	x	
H. femoralis		x	x	
H. gratiosa	x		x	x
H. squirella	x	x	x	
Limnaoedus ocularis		x	x	
Pseudacris nigrita	x			
P. ornata	x			
Rana areolata	x			x
R. catesbeiana	x			
R. grylio				
R. heckscheri	x			
R. sphenocephala	x		x	
Eleutherodactylus planirostris			x	x
Kinosternon bauri	x	x		x
Gopherus polyphemus		x	x	
Rhineura floridana			x	x
Anolis carolinensis		x	x	x
Sceloporus undulatus			x	x
S. woodi			x	x
Cnemidophorus sexlineatus			x	x
Ophisaurus ventralis	x			x
Eumeces egregius	x			x
E. inexpectatus		x	x	x
E. laticeps				x
Scincella laterale		x	x	x
Cemophora coccinea				x
Coluber constrictor	x		x	x
Diadophis punctatus	x			x
Elaphe guttata	x			
E. obsoleta	x			
Farancia abacura	x			
F. erytrogramma	x			
Heterodon simus				x
Lampropeltis getulus	x			
L. triangulum	x			
Masticophis flagellum	x		x	x
Nerodia fasciata	x			
Opheodrys aestivus	x	x		
Pituophis melanoleucus				x
Regina rigida	x			
Rhadinaea flavilata		x		
Seminatrix pygaea	x			
Stilosoma extenuatum	x			x
Storeria dekayi	x			
Tantilla relicta		x	x	x
Thamnophis sauritus	x			
T. sirtalis	x			x
Micrurus fulvius	x			x
Agkistrodon piscivorus	x			
Crotalus adamanteus	x			
Sistrurus miliarius	x		x	x
Total	38	15	24	29

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Table 4. *Amphibian and reptile species collected only by generalized herpetological collecting during the Cross Florida Barge Canal Wildlife Restudy.*

Siren intermedia
S. lacertina
Pseudobranchus striatus
Ambystoma talpoideum
Desmognathus auriculatus
Eurycea quadridigitata
Amphiuma means
Chelydra osceola
Kinosternon subrubrum
Sternotherus minor
S. odoratus
Chrysemys concinna
C. floridana
C. nelsoni
C. scripta
Deirochelys reticularia
Malaclemys terrapin
Terrapene carolina
Trionyx ferox
Ophisaurus attenuatus
O. compressus
Eumeces fasciatus
Drymarchon corais
Heterodon platyrhinos
Nerodia taxispilota

40-50 km/h along secondary roads. Low head light beams are effective in revealing amphibians and reptiles as they cross the road (Klauber 1939). This technique often yields data not otherwise obtainable without unreasonable commitment of time and manpower, especially where secondary, hard-surfaced roads run through habitats of interest. During the Barge Canal study, we recorded 38 species of amphibians and reptiles in 2,903 km of nocturnal road driving. The list includes a number of rare species (*Hyla chrysoscelis*, *Rana areolata*, and *Stilosoma extenuatum*) and three species not otherwise collected during the study: *Farancia erytrogramma*, *Regina rigida*, and *Nerodia fasciata*. Table 3 lists the species collected by this technique and provides a comparison with the other sampling techniques.

Opportunistic Collecting

The four sampling methods allowed us to determine much of the regional herpetofauna, but there were still an additional 25 species that were only opportunistically located during general field activities (Table 4). Thus, although the standardized trapping program, combined with specific activities such as road cruising, quadrat collecting, and time-constrained sampling periods, is effective in providing data on relative abundance of species, seasonal abundance, and relative diversity in different habitats, it does not fully replace the snake collector with potato rake and cloth sack if maximum information on faunal composition is one of the objects of a survey.

Acknowledgments

Our past and present studies of herpetological communities would have been much less successful without the enthusiastic support of numerous individuals; C. R. Smith, H. I. Kochman, and W. S. Lippincott deserve special mention.

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Evaluation of Techniques for Assessment of Amphibian and Reptile Populations in Wisconsin

by

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Abstract

This study was part of a project to develop techniques for sampling terrestrial vertebrates quantitatively and qualitatively by nonspecialized biologists. Drift fences combined with traps proved to be a practical way to uniformly census reptiles and amphibians. Drift fences made from aluminum valley caught more animals per 15 m of fence than those made of either screening or galvanized metal. Aluminum valley is easy to handle and stands up well with continued use. Generally, the more fence set, the more animals caught. Fences shorter than 15 m, however, did not catch enough animals to make their use worthwhile. A height of 50 cm proved effective. A system of 18.9-L traps, 7.6-L traps with funnel rims, and funnel traps were necessary to capture the entire spectrum of amphibians and reptiles in the communities sampled. We believe that several short sampling periods staggered throughout the season are more effective in obtaining an estimate of species composition and populations than a longer sampling period at any one time. Procedures are recommended for using drift fences and traps in various habitats.

Reptiles and amphibians are sometimes difficult to census, as they may remain inactive for weeks if weather conditions are not within their activity range. Temperature, precipitation, soil moisture, humidity, light intensity, wind, and season greatly control their activity patterns. Thus, any census technique must take into consideration the effects of these factors on the animals' biology.

The present study was part of a project to develop techniques for sampling terrestrial vertebrates quantitatively and qualitatively by a nonspecialized biologist. The emphasis was on a uniform sampling method that could be applied to the Till Plain of the northern United States, while maximizing efficiency without losing accuracy.

A number of sampling methods have been used to determine species density and diversity of amphibians and reptiles. Most environmental impact statements give species lists of reptiles and amphibians seen or captured through random search and seize procedures. The success of the techniques varies greatly with the training of the individuals involved, the time of the day and year the collecting is done, the rareness or agility of a species, and the type of habitats sampled. Though fast-moving or secretive species may actually be fairly common, they may not be found if the observer is not looking in the right place. For example, in this study, over 50 h were spent looking for reptiles and amphibians over a 5-year period at the Portage site, but not until drift fences were employed did *Ophisaurus* appear in the sample. Different species vary in their daily and seasonal activity patterns; thus an observer might notice few salamanders above ground on bright, sunny days, no lizards active during a rain, or snakes active on cloudy, windy days. The long-term use of an area must also be considered if habitat has to be destroyed while searching for specimens.

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Population estimates and other quantitative comparisons require extensive search and capture, and often marking. The time of sampling and training of observers are also important. The animals must be marked so that individuals are not counted more than once unless the animals are removed from the population. Salamanders, lizards, frogs, and turtles can all be easily toe-clipped for short-term marking, and snakes can be scale-clipped (Blanchard and Finster 1933; Martof 1953).

Call indices for frogs are of limited use; only mature male frogs call, and in many species only dominant males call. A pond with 18 calling males may have an additional 64 mature subdominants, or may have none, but the population estimate would be the same (Fellers 1975). A call index is, however, a good estimate of the size of the breeding area – the more widespread the calling males, the larger the breeding area. Difficulty in estimating the number of nonterritorial frogs or frogs with very small territories must also be considered. *Hyla crucifer* and *Rana sylvatica* often call in dense choruses numbering in the hundreds. Separating the individual calls is nearly impossible, except possibly by taping and computer analysis.

Frogs are also highly seasonal, and calling is affected by temperature and time of day (see Wiest, this volume). Though only a few frogs may be heard early and late in the season, hundreds may be calling at the peak of the breeding season. In Wisconsin, *Rana sylvatica* calls for only a 2-week interval in early spring. At this time, only *Pseudacris* and *H. crucifer* are also calling. Later in the season *Pseudacris*, *H. crucifer*, *H. versicolor*, and *Bufo* may all be heard calling in the same area, while *Acris* and *R. clamitans* have yet to start. A sampling period would need to cover the entire range of breeding time and on nights of proper temperature and moisture for each species. Its value as a census technique is generally limited to data on species presence. Call differences, however, are the surest way for the nonspecialist to differentiate some species of frogs (e.g., *Hyla chrysoscelis* from *H. versicolor*, or *Rana blairi* from *R. pipiens*).

Fitch (1951) described using funnel traps with and without doors for capturing snakes, lizards, and frogs. He was interested in population dynamics of snakes and set the traps along natural drift fences, e.g., logs and rock ledges. This was an effective method for capturing animals moving along these areas, but choosing such areas requires knowledge of the types of animals being studied. Funnel traps with drift fences were also found to be highly effective by Imler (1945) for bull snakes (*Pituophis*); 1,729 were caught in four summers. Milstead (1959) used drift fences with funnel traps for catching lizards in Texas. Campbell and Christman (this volume) have used funnel traps effectively.

Pit traps of various depths and diameters with and without drift fences have been used in various studies. Covered pit traps are effective in catching lizards (Banta 1957; Lillywhite 1977). Moreover, when they are employed with a drift fence, results have often been exceptional (Shoop 1968; Gibbons and Bennett 1974; Rittschof 1975; B. Hellmich, personal communication; D. Tinkle, personal communication; Campbell and Christman, this volume). Drift fencing seems to be the most effective method of reducing inherent observer bias.

D. Tinkle (personal communication) walked along drift fences and counted animals that came up to the barrier and were trying to move around it. This is satisfactory for long (over 100 m) permanent fences that are irregularly monitored. Short fences (less than 100 m) need restraining devices such as pit and funnel traps associated with them to be effective.

Although drift fences and traps are more cumbersome and expensive than walking a line transect or searching a quadrat, these drawbacks are more than compensated by the elimination of the observer and temporal biases. Because of its effectiveness and efficiency, the drift fence and trap method seem the best way to standardize sampling of reptile and amphibian communities.

The present study, undertaken from April through November 1976, was devised to test different aspects of drift fences with pits and fun-

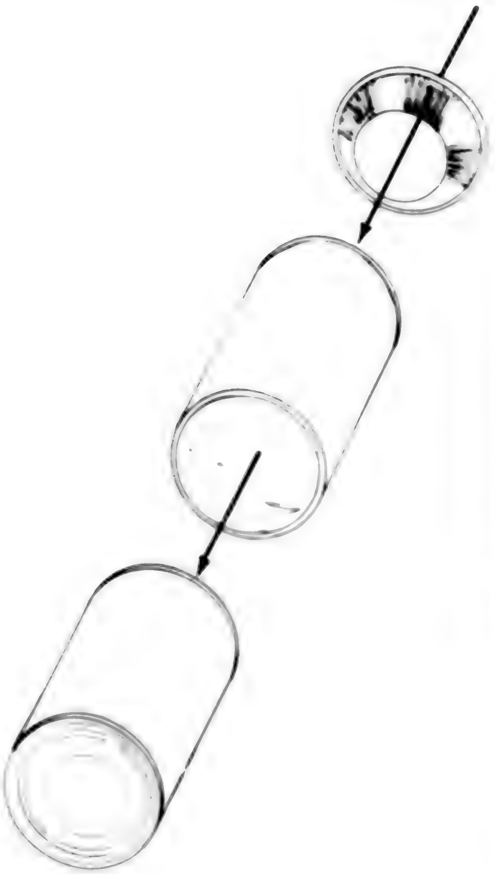

Fig. 1. Construction of a 7.6-L pit trap with funnel.

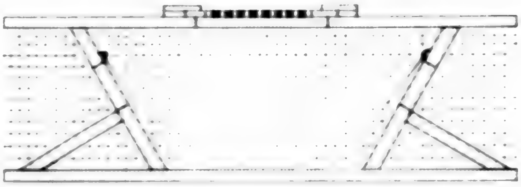

Fig. 2. Funnel trap (after Fitch 1951).

Fig. 3. Drift fence made from aluminum valley. Note bend in fence around a rock (Point Beach, Line A).

nels. The materials, length, height, and positioning of fence, the size and type of pits and funnel traps, the season and weather, and the length of time needed to sample were tested to formulate a standardized method.

Materials and Methods

The sampling unit is defined here as the length of the drift fence. In the text, drift fence refers to either the fence alone or the drift fence with its associated traps. The exact meaning should be clear from the context.

The following materials were tested for fencing and traps: aluminum valley (or flashing), 15-m roll, 50 cm high; aluminum window screen, 15-m roll, 60 cm high; galvanized sheet metal, 3 m by 60 cm; 3.8-L cans with funnel rims; 7.6-L cans made by cutting the bottom out of one can and securing two cans together with 7.5 cm duct tape (Fig. 1); plastic bowls with bottoms removed for attachment to 3.8-L and 7.6-L cans as funnel rims (Fig. 1) and bowl lids; 18.9-L plastic ice cream buckets with lids; 18.9-L metal paint cans with lids; and two-door funnel traps (Fig. 2).

Drift fences made from the aluminum valley were set up in either 15 or 30-m lengths in a 10-cm trench (Fig. 3) with a galvanized metal stake set at each end of the valley. The aluminum screen was set in 7.5 to 30-m lengths, buried 10 cm underground, and staked with wood lathe every 2 m. The galvanized metal sheets were fastened together, buried 15 cm underground, and staked with galvanized angle iron between each sheet (Fig. 4).

A combination of funnel traps and the following types of pit traps were used: 3.8-L cans with and without funnel rims, 7.6-L cans with and without funnel rims, and 18.9-L buckets. Traps were set at various distances along the fence. Pit traps were buried flush with the surface of the soil, and funnel traps were set against the fence and tight against the soil. Traps were checked at least every other day, and all animals were marked and released 3 m on the opposite

Fig. 4. Drift fence made from galvanized metal (Blue River, Line 1).

side of the fence. If weather conditions were not right, covers were placed on pit and funnel traps until the weather became more suitable.

Test trap lines were set up with the same number of each type of trap on both sides of the fence. The low number of animals caught did not warrant the rotation of trap positions. All trapping of reptiles and amphibians was conducted in 1976 unless otherwise designated. Scientific and common names for reptiles and amphibians encountered in the study are listed in the Appendix.

Study Areas

Three main habitat types were used for testing various aspects of drift fencing in southern Wisconsin: oak-hickory woodlots, wetlands, and old fields and prairie. A short period of trapping was also conducted in mixed deciduous forest.

Oak-Hickory Woodlots

These areas were chosen to compare results of reptile and amphibian sampling in an area where small mammals, birds, and vegetation were also being censused. Small deciduous woodlots in southern Wisconsin are not notably productive of a high diversity of reptiles or amphibians. The effectiveness of 3.8-L vs. 7.6-L pits and the position bias of the fence were tested at these sites. Traps were open for 24 days, between 27 April and 21 May.

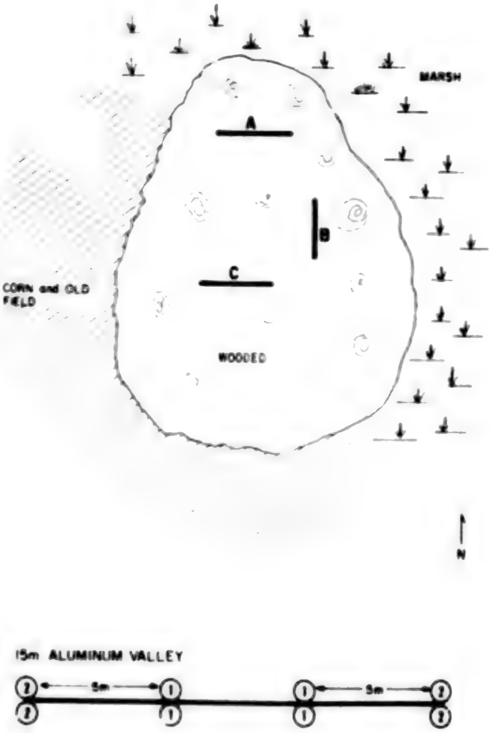

Fig. 5. Shaw Marsh site, Wisconsin. All three lines were constructed in a similar fashion. The symbols 1 and 2 refer to the positions of 3.8 and 7.6-L pit traps.

Shaw Marsh Woodlot, Dodge County (T11N R14E, Sec 22 NW 1/4)

This oak-hickory forest (Fig. 5) had a mean of 245 trees (≥ 10 cm diameter) and 746 saplings per ha. There was a dense herbaceous understory with many fallen logs, mostly elm, which provided excellent cover for woodland amphibians and reptiles. The forest was bordered by a cattail marsh and an intermittent stream on the north and east. To the south and west it was bordered by cornfields and an old field.

Busse Tract, Columbia County (T12N R12E, Sec 22 SW 1/4)

This oak-hickory woodlot (Fig. 6) had a mean of 264 trees and 469 saplings per ha. A small irrigation ditch and canary grass field were to the west and north of the woods. A young (6 to 8 years) pine plantation was on the east and a cornfield on the south.

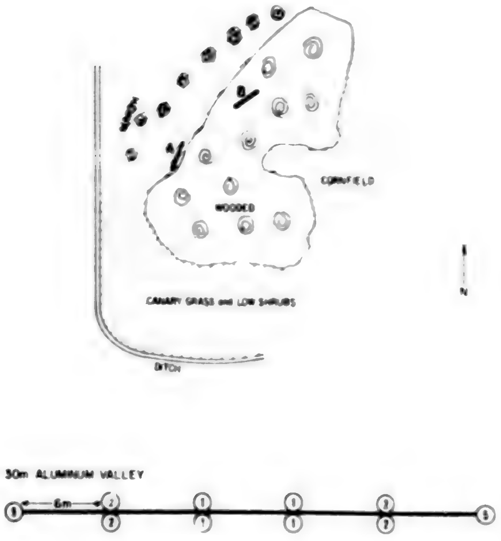

Fig. 6. Busse Tract site, Wisconsin. Both lines were constructed in a similar fashion. The symbols 1, 2, and 5 refer to the positions of 3.8, 7.6, and 18.9-L pit traps.

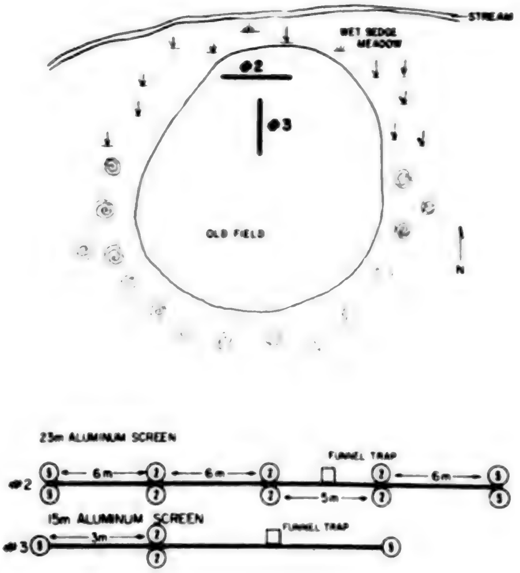

Fig. 7. Portage A site, Wisconsin. The symbols 2 and 5 refer to the positions of 7.6 and 18.9-L pit traps.

Wetlands and Old Fields

Portage site, Columbia County (T12N R9E, Sec 28, 33: T11N R9E, Sec 4)

Drift fences and traps were set in three old fields adjacent to wetlands and around a woodland pond. All four sites were on the land of Wisconsin Power and Light Coal Generating Plant, south of Portage. Traps were monitored from 22 April to 3 November. These lines were set to test position bias, effectiveness of trap types, and length and type of fence.

North Knoll – old field along Duck Creek (Fig. 7). – The area was bordered by a lowland hardwood forest to the south and sedge meadow to the north. During the spring, the sedge meadow is flooded by Duck Creek.

North Knoll – adjacent to the Intake Channel (Fig. 8). – This area was an old field adjacent to a short strip of marsh about 50 m wide adjacent to the intake channel from Duck Creek to the Power Plant. It was bordered on the east and west by lowland hardwood forest and to the south by a large sand blow which was used for nesting by turtles.

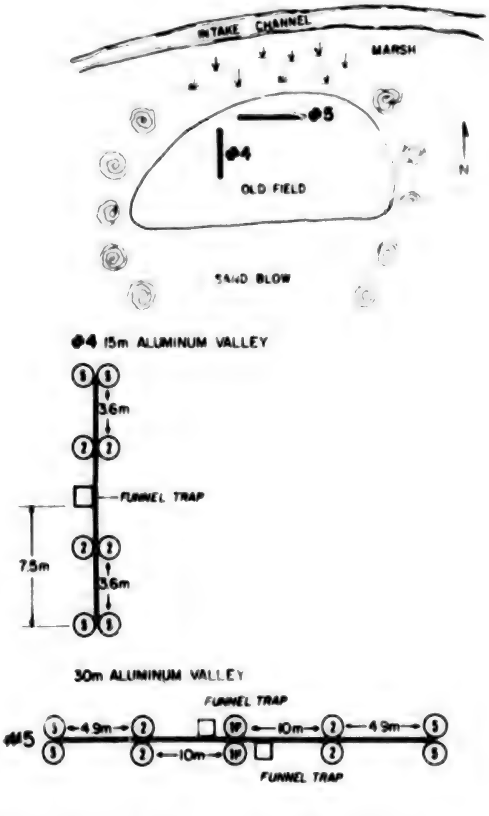

Fig. 8. Portage B site, Wisconsin. The symbols 2, 5, and 1F refer to the positions of 7.6 and 18.9-L pit traps and 3.8-L pit traps with funnels.

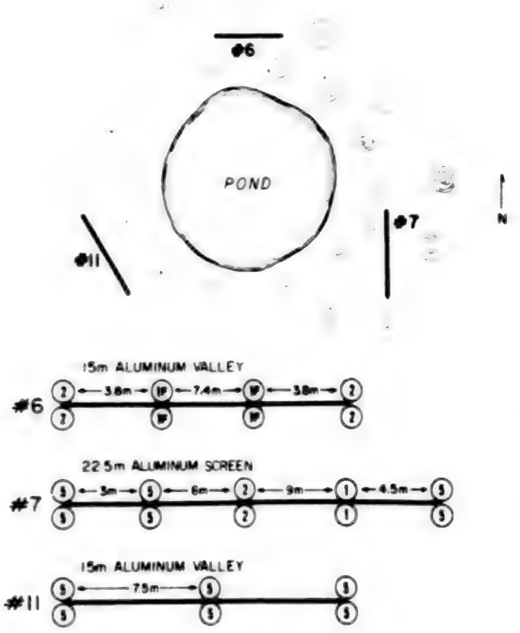

Fig. 9. Portage C site, Wisconsin. The symbols 1, 2, 5, and 1F refer to the positions of 3.8, 7.6, and 18.9-L pit traps and 3.8-L pit traps with funnels.

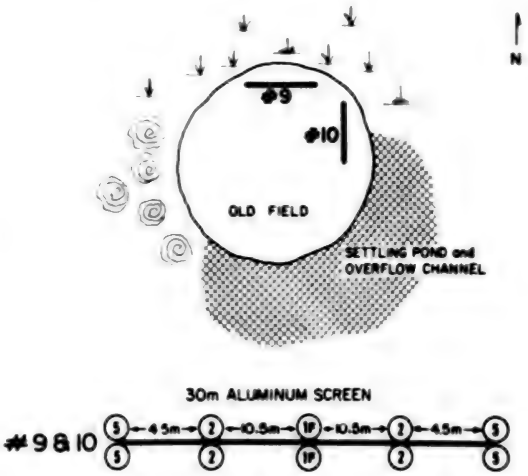

Fig. 10. Portage D site, Wisconsin. The symbols 2, 5, and 1F refer to the positions of 7.6 and 18.9-L pit traps and 3.8-L pit traps with funnels.

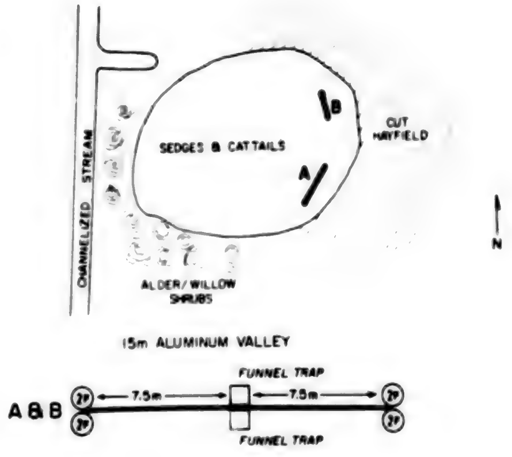

Fig. 11. Long Lake site, Wisconsin. The symbols 2 F refer to the positions of 7.6-L pit traps with funnels.

North Knoll – Woodland Pond (Fig. 9). – Three pieces of fencing were installed on the north, east, and west sides of a woodland pond, 3 m from the shore. The pond was about 30 × 30 m and 1.5 m deep, surrounded by a young oak, hickory, and paper birch woods.

South Knoll (Fig. 10). – This site was in an old field on clay soil adjacent to a small cattail marsh to the north and a lowland hardwood forest to the west. The east and south borders of the field were bordered by the settling pond and overflow channel.

Long Lake, Manitowoc county, (T19N R21E, Sec 6)

The northeast edge of the lake was bordered by a cattail marsh and an alfalfa field upland from the cattails (Fig. 11). This area was chosen to test the efficiency of drift fences versus hand capture. Between 1 April and 10 September, 200 man-hours were spent by another researcher marking frogs in the area. Because of dry soil conditions, the two 15-m aluminum drift fences were set 5 m from the alfalfa field in the marsh, and traps were open for 12 days in September and October.

Prairie

Blue River Cactus and Dunes, Grant County, (T8N R1W, Sec 6 E 1/2)

This 52.6-ha area featured a variety of xeric plant community types including sand blows, active dunes, flat sand barrens, and stabilized dunes forested with oaks (Fig. 12). *Hudsonia* is

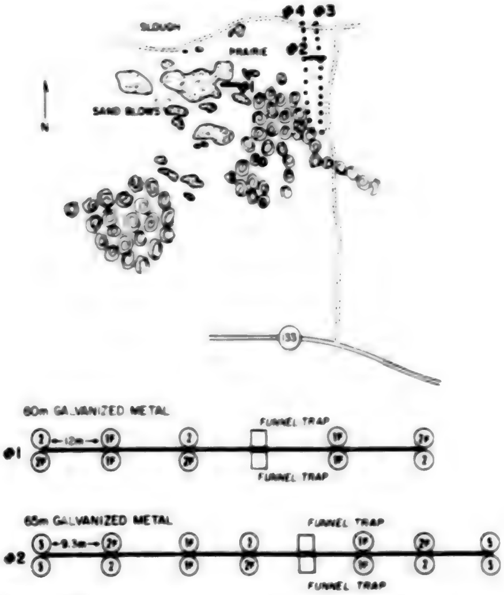

Fig. 12. Blue River site, Wisconsin. The symbols 2, 5, 1F, and 2F refer to the positions of 7.6 and 18.9-L pit traps and 3.8 and 7.6-L pit traps with funnels.

abundant; other dune binders include *Arctostaphylos*, *Selaginella*, fungi (*Geaster*), mosses, and green algae. Two succulents, *Talinum rugospermum* and *Opuntia compressa*, occurred here. Nearly 12 ha were forested with oaks, often with an understory dominated by *Carex*. The soil type was Sparta loamy fine sand. It is almost certain that the area was once cultivated; subsequent wind erosion and loss of fine soil particles resulted in abandonment of the land.

Two fence and trap systems were set (Fig. 12). Line No. 1 was near the southeast end of a large sand blow (Fig. 4). Line No. 2 was in the northeast corner of the area in the center of the sand prairie and 3 m from the dirt road at the boundary. The traps were open for 85 days, between 26 May and 25 August.

Ten funnel traps, facing north-south, were set 20 m apart in a transect perpendicular to the center of drift fence No. 2 (position No. 3 on Fig. 12). After two weeks, the transect was moved to the west edge of drift fence No. 2 (position No. 4 on Fig. 12). These transects were run to determine the feasibility of using funnel traps without drift fences and also to see how far individual lizards moved within the study area.

Spring Green Reserve, Sauk County (T8N R4E, Sec 5, 6)

This area consisted of 113.3 ha of sand barrens – prairie and old fields bordered by a dry-lime prairie and a southern dry-mesic forest on the hills on the northern boundary, with crop lands on the east, south, and west borders (Fig. 13). There was no temporary or permanent water or wetlands within a 2½-km radius. Position of fence, type of trap, and movement of animals were being tested at this site. Relative numbers of each species were known from work over the previous 15 years by one of us (RCV). Three species of lizards, seven species of snakes, and one species of turtle were known to inhabit this area. This area was chosen to test the trapping procedure on an area of high species diversity and known species composition.

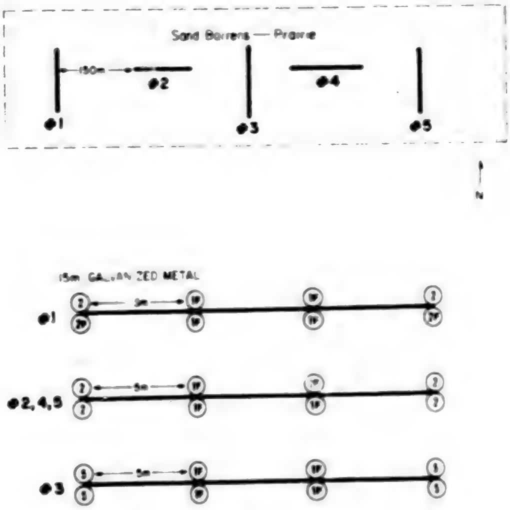

Fig. 13. Spring Green site, Wisconsin. The symbols 2, 5, 1F, and 2F refer to the positions of 7.6 and 18.9-L pit traps and 3.8 and 7.6-L pit traps with funnels.

Mixed Deciduous Forest

Point Beach State Forest, Manitowoc County, (T20N R25E, Sec 29)

This area was a mixed deciduous forest with a dense canopy and thick understory of herbaceous plants and mulch (Fig. 14). The area was used to test the use of drift fences, as opposed to counting frogs in quadrats, and to check the reliability of drift fences in determining species composition. Three adjacent 9 × 9-m quadrats (1, 2, and 3, Fig. 14) and one separate quadrat (4, Fig. 14) were censused by another experienced investigator who walked back and forth counting frogs for 2.5 h.

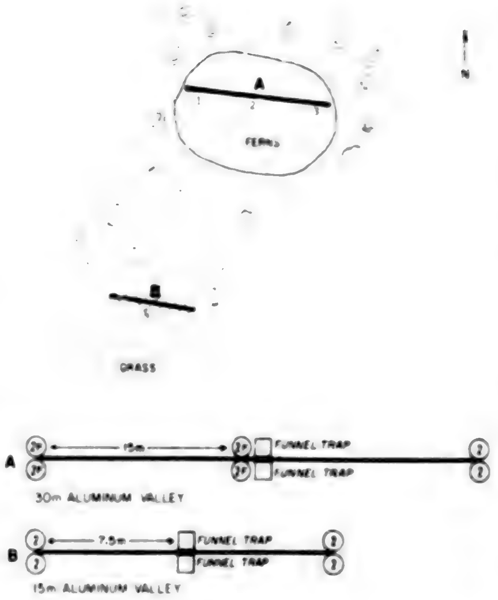

Fig. 14. Point Beach site, Wisconsin. The symbols 2 and 2F refer to the positions of 7.6-L pit traps and 7.6-L pit traps with funnels.

Evaluation of Drift Fence Trap Techniques

Effectiveness of Fencing Materials

The traditional measurement for animals caught in traps is number caught per trap day. Drift fences made from aluminum screening caught a slightly greater number of reptiles and amphibians per trap-day than did fences made of either aluminum valley or galvanized metal (Table 1).

In testing the various fencing materials, however, the number of animals caught per trap-day was not the best measurement of effectiveness, since the number and size of pit traps associated with individual fence lines were variable. Therefore, the unit of measurement regarded as most reliable was number of animals caught per 15 m of fence (Table 1). This new measurement of effectiveness showed a slightly greater number of animals caught with drift fences made from aluminum valley than with aluminum screen (33 and 31 animals per 15 m of fence-day × 100, respectively).

Fences caught all forms of reptiles and amphibians regardless of fencing material. A potential drawback to the screen is the ability of some animals to crawl over it. This may have happened with the salamanders – only six salamanders were caught in 120 m of screen, whereas 18 were caught in 7.5 m of aluminum. On three occasions, garter snakes were seen going over the screen fences, once without being pursued and twice when an observer was walking along the fence. The same size snakes were never seen going over the aluminum. The use of numerous stakes along the screen fence provided "ladders" for many small snakes, lizards, and salamanders to work their way over the fence. This was not a problem with aluminum. Galvanized metal used at Blue River was an effective barrier to all forms known to inhabit that prairie and caught animals at the rate of 12 animals per 15 m of fence-day × 100 (Table 1).

Table 1. *Numbers of animals caught with different drift fence materials in southern Wisconsin.*

	Portage Area		Blue River Area
	Aluminum valley	Aluminum screen	Galvanized metal
Frogs and toads	154	228	–
Salamanders	18	6	–
Snakes and legless lizards	69	114	167
Turtles	15	11	–
Total	256	359	167
No. traps	35	46	28
No. trap days	5,198	6,550	4,760
Animals/trap day × 100	4.9	5.4	3.5
No. 15-m lengths of fence	5	8	8
No. 15-m fence days	733	1,145	1,360
Animals/15-m fence-day × 100	35	31	12

Evidence from trails in the sand showed no snakes or lizards going over the fence. However, these results are not directly comparable to the catch with the other two fence materials, because of the habitat differences of the study areas.

Screen weighs much less than the solid aluminum and is a little easier to carry; a roll of aluminum weighs about 9 kg and rolls into a cylinder 41 cm in diameter. It has nearly the same flexibility as screen for going around logs, trees, and rocks. Though aluminum needs a stake at each end only, screen requires staking at least every 3 m or the fence sags and animals crawl over it more easily. Aluminum stands up better over continued setting and pulling of fences; screen tends to tear and get matted with dirt and debris. The galvanized metal is excellent for a permanent fence, but there are disadvantages since the sheets weigh about 20 kg apiece and cannot be rolled and transported easily.

Length, Height, and Position of Fence

Fence lengths of 3-60 m were tested. Generally, the more fence set, the more animals caught. Drift fences shorter than 15 m, however, did not catch enough animals to make their use worthwhile.

A comparison of the catch along two pairs of 30-m and 15-m lengths of fence, set perpendicular to each other, was made in two old fields at Portage (Table 2). Twice as much fence resulted in the catch of about twice as many animals. Two 30-m sections set perpendicular to each other in a third old field caught comparable numbers of animals.

Since a fence must be high enough to discourage snakes from attempting to crawl over it or adult frogs from jumping over it, there is some optimum height needed to ensure the effectiveness of the fence and still maintain a manageable size. The minimum height used (50 cm) was sufficient to capture two 20-cm fox snakes, seven snakes over 40 cm, and hundreds of small snakes. Anything higher than this would be very unwieldly and is apparently not necessary for a census method.

Table 2. *Comparison of numbers of animals caught in a 5-month period with 30-m and 15-m lengths of drift fence at the Portage site.*

	Lines 2 & 3		Line 4		Lines 9 & 10	
	30 m	15 m	30 m	15 m	30 m	15 m
Snakes	76	20	38	23	9	9
Turtles	7	2	4	0	1	1
Frogs and toads	90	83	49	22	20	14
Total	173	105	91	45	30	24
Animals m	6	7	3	3	1	1.5

There were often considerable differences in catch along various sections of fence within the same field and between adjacent fence lines. For example, at Portage (location No. 5) on 12 October, one 18.9-L pit trap caught 14 snakes, whereas the other 9 pit traps and 2 funnel traps caught a total of only 5 snakes. Other differences in catch between fence lines in similar habitats are given in Table 3. Position of fence is especially important for migrating reptiles and amphibians. Fences set parallel to diverse habitat boundaries are more likely to pick up migrating animals than those set perpendicular to them, as animals are often moving across vegetation gradients (i.e., into or out of ponds, marshes, nesting grounds, and hibernacula). At Portage A, the northern marsh side of line 2 produced only 19 snakes, while the upland side had 48. However, line 3, set perpendicular to line 2, showed no difference in the number of snakes on either side of the fence (Fig. 7).

The catches of amphibians from the same fences, however, differed. Line 2 had no difference in the number caught on either side (40 vs. 49), but on line 3, 68 amphibians were caught

Table 3. *Differences between catches of selected groups of reptiles on different sampling lines in three similar habitats in southern Wisconsin.*

Location and group	Line number 1	2	3	4	5
Blue River					
Elaphe vulpina	4	0	–		
Heterodon	3	0	–		
Chrysemys	14	0	–		
Emydoidea	7	0	–		
Cnemidophorus	108	58	–		–
Portage					
Ophisaurus	–	–	–	2	0
Spring Green					
Cnemidophorus	10	0	0	2	13

on the east side and only 16 on the west side (29 of the 68 were *Rana pipiens* caught on a single day after a rain on 5 October). It is possible that the frogs were moving toward Duck Creek, a potential hibernaculum, which is on the west side of the fence.

At Portage B, line 5 showed no side bias for snakes or amphibians; line 4 had no side bias for snakes, but 18 of 21 amphibians were caught on the west side of the fence (Fig. 8). These examples show the importance of fixed migration patterns and the necessity for fences to be set as barriers in all directions to obtain the best sample.

Spring migrations of *Bufo* were obvious at both Shaw Marsh and Busse Tract. Catches at Shaw Marsh (Fig. 5) on 17 May indicated a definite movement towards the marsh. Thirty-four, 11, and 11 *Bufo* were caught on the sides of lines A, B, and C that faced away from the marsh, whereas 0, 6, and 5 were caught on sides nearest the marsh. The Busse woods (Fig. 6) showed the same phenomenon the same day—40 *Bufo* were caught on the eastern woods side of line A and 9 on the marsh side, and 19 *Bufo* were caught on the southeastern woods side of line B and 6 on the marsh side.

The Busse Tract also showed the desirability of placing several fences in different areas. On 9 July no amphibians were caught on line B in the woods, but 37 *Bufo* were caught on line A, all on the marsh side of the fence (all newly transformed young dispersing from the breeding ponds).

Types of Traps

Six different types of traps were set along drift fences to determine which were most effective and efficient (Table 4). Different kinds of reptiles and amphibians showed strikingly different responses to the various trap types.

Funnel traps were clearly more effective for catching lizards than pit traps. Of the pit traps, 18.9-L and 7.6-L traps with funnel rims were more effective than the 7.6-L traps without funnel rims (generally twice as many lizards caught) or 3.8-L traps with funnel rims.

Funnel traps were also effective for catching snakes. At Blue River, nine snakes, most over 40 cm, two over 1.2 m, were caught in funnel traps. Only one larger than 19 cm was caught in a pit trap. Similarly, in the Portage old field, all seven snakes over 40 cm were caught in funnel traps. The 18.9-L cans were superior to the 7.6-L cans. The 3.8-L cans with funnel rims were also ineffective for snakes. Salamanders and frogs were rarely caught in funnel traps, but pitfalls were effective. Amphibians were caught in similar numbers in 7.6 and 18.9-L rimless pit traps, tested at the Portage sites. The 3.8-L cans with funnel rims caught a negligible number of amphibians. At the woodland pond site at Portage, the use of 3.8-L traps with funnel rims vs. 7.6-L traps without funnel rims was tested; the 7.6-L traps caught almost 10 times as many amphibians as the 3.8-L traps with funnel rims. Adult green frogs were observed at Blue River escaping from 7.6-L traps without funnel rims, but not out of the same sized traps with rims. However, 7.6-L traps without funnel rims worked well for juvenile frogs.

There was no difference in the catchability of frogs and toads between 3.8, 7.6, and 18.9-L pit traps, all without funnel rims, at the Busse Tract, but at Shaw Marsh there was a much higher catch in the 3.8-L traps. Although there were numerous tree frogs calling at Portage in the spring, very few were collected. This may be due in part to the location of the majority of fences outside the woods, or to the ability of the frogs with their adhesive feet to crawl readily over fences and out of pit traps.

The 18.9-L cans are necessary for capturing large adult turtles. Fifteen of the 21 adult turtles caught at Blue River were in the four 18.9-L buckets. Four turtles fell into the 12 7.6-L cans and 2 jammed their shells into the 3.8-L cans with funnel rims. Portage showed a similar pattern: 9 turtles in 30 18.9-L, 11 in 26 7.6-L, and 3 in 10 3.8-L traps. Hatchling turtles at both areas fell readily into any size pit. They were caught in both 7.6 and 3.8-L traps with funnel rims at Portage line No. 6.

In summary, 18.9-L pit traps are necessary for trapping adult turtles and are highly effective for small snakes and amphibians and lizards. The 7.6 and 18.9-L traps were effective for frogs and lizards, but the addition of the funnel rim on the 7.6-L traps (Blue River and Spring Green) appeared to yield an even higher catch. Funnel traps are best for lizards and are the only suitable trap for large snakes. The 3.8-L cans were unsuitable, except for some hatchling turtles and toads. A system of 18.9-L traps, 7.6-L traps with funnel rims, and funnel traps seems

Table 4. *Effectiveness of funnel traps and different sizes of pit traps set along drift fences for catching amphibians and reptiles.* Animals caught expressed as number caught/trap day × 100.

	Pit Traps					
Animal group and area	3.8 L	3.8 L (with funnel rims)	7.6 L	7.6 L (with funnel rims)	18.9 L	Funnel traps
Lizards						
Blue River (340–680 trap days)	-	4.5	3.1	7.2	6.5	16.4
Spring Green (80–800 trap days)	-	0.8	1.9	7.5	0	5.4
Snakes and Legless Lizards						
Portage (540–3,780 trap days)		0.3	0.6		4.6	2.4
Blue River (340–680 trap days)		0	0	0	0.2	2.6
Frogs and Toads						
Blue River (340–680 trap days)		0	0.5	2.1	1.7	0.2
Portage (540–3,780 trap days)		0.4	3.0		3.3	0.6
Shaw Marsh (288 trap days)	23.0		9.7			
Busse Tract (96–192 trap days)	33.3		29.2		30.2	
Salamanders						
Portage (540–3,780 trap days)	–	0.3	0.2		0.4	0.4
Turtles						
Portage (540–3,780 trap days)	-	0	0.2		0.3	0
Blue River (340–680 trap days)		0.3	0.8	0	4.4	0

necessary to capture the spectrum of amphibians and reptiles in a community, although tree frogs were not adequately sampled by any of our methods.

Effect of Weather and Season

Precipitation markedly affects the activity of amphibians and reptiles. In 1976, Wisconsin experienced the worst drought in 40 years. When there was rain, amphibians moved immediately (Fig. 15). For example, before the rain, 0-5 animals were caught per 2-day interval at Portage, and 1-2 at Busse Tract and Shaw Marsh. On 15-16 May, 3.8 cm of rain fell; the response was 12 animals at Portage (Fig. 15), 69 at Busse, and 67 at Shaw. At Point Beach on 4 October, 18 frogs and 1 salamander were caught; after 1.1 cm of rain on 5 October, 257 frogs and 7 salamanders were caught within 24 h. Similar responses to rain were noted at Blue River (Fig. 15).

Lizards and snakes, unlike amphibians, often moved about 2 to 3 days after precipitation, whenever temperatures rose. The 5 October rain at Portage produced 97 amphibians and reptiles (mostly frogs), but on 12 October, several days after the rain, the temperature rose and 38 snakes were caught.

Both rain and temperature affected not only estimates of the presence of species, but also determinations of population levels (26 June-5 July). The movement of lizards at Blue River was highly erratic, due primarily to the summer weather conditions. Drought and high temperatures forced lizards to remain underground for

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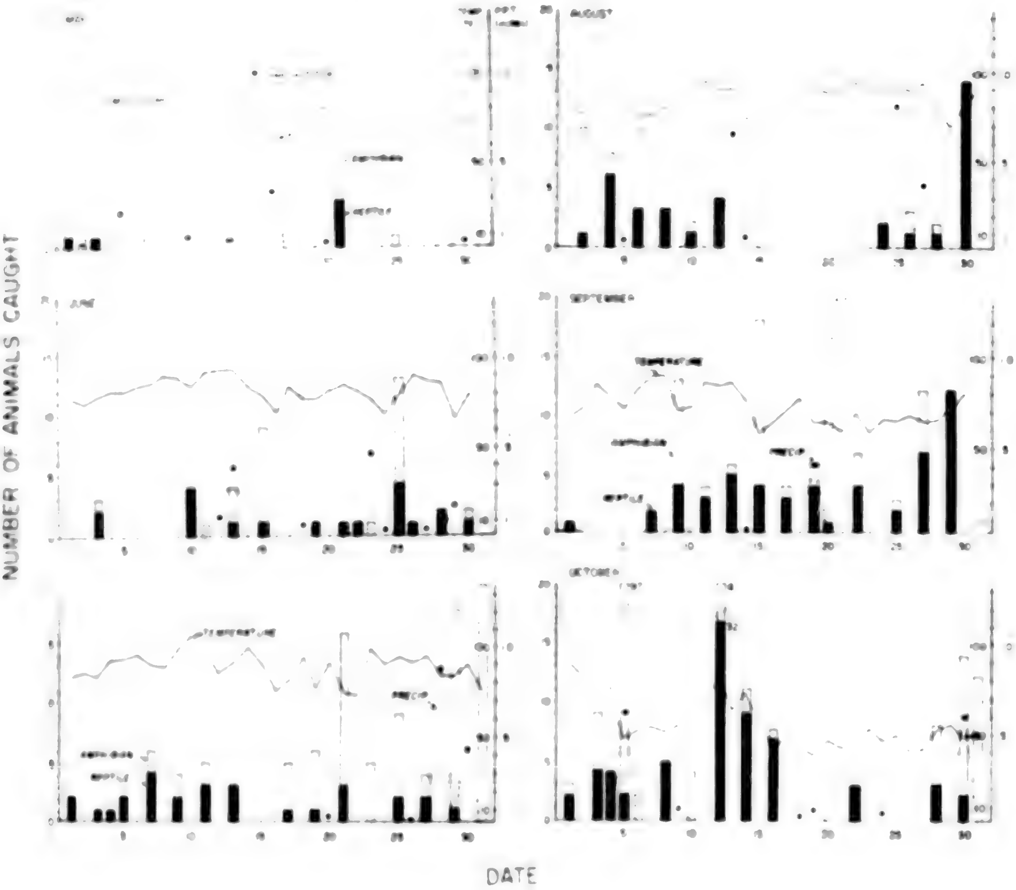

Fig. 15. Relation between catch of all reptiles and amphibians at Portage, Wisconsin, and precipitation and temperature.

days; after a rain, however, there was much more activity than normal, resulting in high population estimates (Fig. 16). A 4-day sample gave as accurate a population estimate as a 15-day sample. Normally, individual *Cnemidophorus* are active for a day or two of feeding, then retreat underground for a couple of days.

Spring and fall dispersal and migrations are also responsible for increased activity. At Blue River in mid-August there was an abrupt rise in the catch of lizards (Fig. 16). Most of these were hatchlings just emerging. Although the adults became inactive for the year at this time, the young remained active until mid-September.

Post-metamorphic migrations of toads were seen on the Busse Tract in early July, when 38 toads were caught along one side of a drift fence in one night. All were newly transformed and dispersing from the breeding ponds. The same phenomenon was observed at Portage in late August, when the large number of snakes caught were mostly young of the year, presumably wandering away from their place of birth.

Amphibians and reptiles move to winter hibernacula in September and October. At Portage, more animals were caught in the fall following rain than in summer under similar conditions. In August and September, hatchling turtles were caught moving from the nesting sites to water.

Many species of salamanders spend most of their time underground or under cover, and their presence is usually known only during dispersal or migration times. This was apparent at Portage, where the only two *Ambystoma tigrinum* recorded were caught in late fall. Turtles caught at Portage and Blue River were aquatic, but females must come to land to lay eggs from late May to early July.

High numbers of amphibians and reptiles

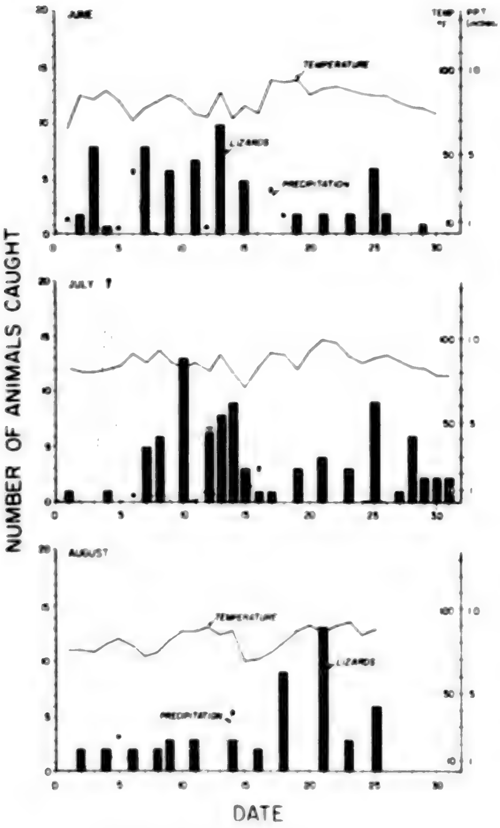

Fig. 16. Relation between catch of *Cnemidophorus* at Blue River and precipitation and temperature.

caught after spring and fall rains may not necessarily indicate large populations in the habitat where they are caught. They often travel a mile or more from summer foraging grounds to winter hibernacula, and many unsuitable foraging areas are often traversed enroute. Better estimates of the number of snakes, lizards, or frogs in a particular habitat can be obtained in June and July, after the spring migrations and before the appearance of young.

Length of Trapping Period

Because of seasonal activity, staggered reproductive strategies, and migration patterns, it is impossible to adequately sample all species present in an area at the same time. Thus, the length of time necessary to obtain a good estimate of the diversity of animals present is an important factor in evaluating any census method.

Density and diversity of frogs, snakes, and turtles at Portage and turtles at Blue River were high and the trapping periods long; thus the trapping time needed to show species composition and abundance at different seasons could be determined by examining the catch over the entire period. At Portage, drift fences were in operation for 162 days, but only 3-5 continuous days of trapping during optimum weather conditions were needed to capture the most common species of reptiles and amphibians.

The three most common species of turtles were taken in 3 days during the laying season in June at Portage. The fourth species, *Trionyx spiniferus*, was not caught in the nesting season but was taken during the August posthatching dispersal. In 2 days at Blue River, two of the four species of turtles known to nest in this area were caught. The other two never appeared, but they are less common.

In mid-summer, 1 to 3 months of continuous trapping were required at each trapline at Portage to take the four common species of snakes, whereas the same four species were caught in 1 to 4 days in September and October. Summer trapping of the three common species of frogs at the Portage sites required over 1 month, whereas all three were often caught on a single day or at least within 3 days in September and October.

Racerunner population estimates were made with the Jolly stochastic model (Jolly 1965). Catches for 4-day intervals from 30 May to 28 July ranged from 0 to 75, whereas those from three 15-day intervals ranged from 29 to 60 during that time. Omitting the two periods of no catches yields a 4-day interval range of 22 to 75, which is roughly comparable with the estimate given by 15-day intervals.

The catch of all species over the months of trapping in this study showed many periods of low or no success. Since movement normally is associated with favorable weather and migration activity, several short sampling periods staggered throughout the season should give a better estimate of species composition and populations than a longer period at any one time.

Overall Effectiveness

Overall effectiveness of the fence-trap systems was measured through comparison of catches in areas of known species composition and in areas which were being sampled by other methods. The species composition at the Portage sites has been known from 5 years of searching. All these species at Portage were also taken through drift fence trapping. Also, two species (the glass lizard and tiger salamander) that were recorded in previous years only near Portage were also trapped by drift fences.

At Point Beach, in 5 days of trapping without rain, 3 of the 10 known species of amphibians in the forest were caught. In 5 days, during which a rain occurred, 6 of the 10 were caught. Of the two species not caught by traps one is normally uncommon and the other was uncommon because of the drought.

The drought conditions apparently affected the sampling at Spring Green. In 2 months of trapping, only 2 of the 12 known species of reptiles in this area were caught. In 15 h of intensive searching in the area during the summer, however, only three species were found.

Two of our study areas were being studied by other researchers. At Long Lake, B. Hellmich (personal communication) marked 420 leopard frogs from 1 April to 10 September. Nearly all of these were caught in an alfalfa field rather than in a marsh, and he estimated the population to be 4,004 individuals. Although about 75 leopard frogs were seen in the alfalfa field at the time the fence-trap systems were set up in the adjacent marsh, only four were caught in two 6-day trapping periods. This illustrates the need of setting several fences throughout an area in various habitats. Hellmich also saw about 20 toads, 30 green frogs, and 70 wood frogs (mostly in the marsh) in the area. While trapping in each of the two 6-day intervals, we caught 3 of the 4 anuran species known from the area. Thus the use of drift fencing to determine species composition appears to be effective.

Before the trapping system was set at Point Beach, all the *Rana sylvatica* were censused in two 9 × 27-m areas by walking back and forth and counting frogs. In 2 h and 46 min, 120 *R. sylvatica*, mostly juveniles, were found in area A and two in area B. Drift fence line A (30 m) produced 75 *R. sylvatica* and line B (15 m) produced 20. The difference between the catches and the frog counting represents time-of-day bias. Counting was done from 1512-1758 CDT, whereas the traps were open for 24 h. When a trained person walked back and forth across the quadrat, more frogs were seen, but some of them could have been counted more than once. The drift fence was stationary and caught only the frogs moving to it. Collecting proceeded 24 h day with little effort after the initial set-up, and with little observer bias. Therefore, many areas can be compared by different people during the same time span and relatively comparable data can be obtained.

Population estimates (Jolly 1965) of the number of six-lined racerunners caught at line 2 at Blue River ranged from 0 to 75 ($\bar{x}$ = 36) for 11 4-day intervals. This compares with 45 *Cnemidophorus* caught by the fence during the same time period. If the two 4-day periods when population estimates were zero due to severe weather conditions are eliminated, then the mean population estimate corresponds closely to the actual number caught over the summer (45 compared to $\bar{x}$ = 44 estimated).

The transect of 10 funnel traps set perpendicular to Blue River fence No. 2 caught marked animals a maximum of 20 m from the fence. Since the next traps were 40 m on each side of the fence, these results suggest that a drift fence collects from an area less than 80 m wide for relatively sedentary species such as *Cnemidophorus*. Funnel traps without drift fences were effective for capturing *Cnemidophorus*: 36 captures in 10 traps over a 41-day period compared with 45 in 60 m of fence with 12 traps. Funnel traps without fences seem to be an effective way of sampling some lizard populations. Further trapping is needed to compare population estimates.

Manpower and Cost

The most time-consuming part of running drift fences is set-up time. It took two people 1½ h each to establish 30 m of aluminum fence with 8 pit traps and 2 funnel traps. A dozen animals were removed and marked from 15 m of fence in 5-10 min. Even when large numbers of animals were caught, removal time was relatively short. For example, 267 animals were removed from 41 m of fence and marked by two people in less than 1 h. Distance between trap lines dictated the number which could be checked per day. A site with a total of 90 m of fence would require ½ day to set up, and could be checked in less than 1 h by one person; moreover, if the sites were less than an hour apart four sites could easily be done per day.

Once the fence was established, it was convenient to leave it open only during ideal weather conditions, particularly when several sites 25-50 km apart are being monitored. Funnel traps were picked up and pit traps covered when not in use. A 15-m fence with pit and funnel traps was removed by one person in 5 min. The initial cost was about $50 for 30 m of fence with traps. However, the fence can be used for many areas. Operating cost for eight sites would be about $1,200 for an entire season.

Recommended Procedures

Materials

Although somewhat more costly and heavier to carry than screening, aluminum valley seems to be the best fence material. It should be more economical over longer periods since it is far more durable than screen. Hardware cloth was not used because of the same disadvantages of the screen and it costs as much as aluminum valley. C. R. Shoop (personal communication) has been using a plastic-coated screen successfully for salamanders in Massachusetts. It is lighter than aluminum and less expensive, but its durability needs testing.

The following materials are recommended for fencing and traps: aluminum valley (or flashing), 1-m angle iron stakes (two per fence line), 18.9-L plastic ice cream buckets with lids, 7.6-L cans with funnel rims (Fig. 1) and lids, and two-door funnel traps (Fig. 2).

Time of Trapping

Season

In Wisconsin, from 1 April through 15 June, all of the species of reptiles and amphibians using a terrestrial habitat may be expected to be active. Trapping in the early part of April is necessary to collect many terrestrial and fossorial salamanders (*Ambystoma maculatum*, *A. laterale*, *A. tremblayi*, and *A. tigrinum*). A trapping period in early September will also produce these species when the young are leaving the ponds. However, in dry years, reproduction may not be successful, and a fall trapping period would not be necessary.

Trapping in late April–early May yields fewer species of salamanders, but most species of frogs and many snakes are moving. In late May, most species of snakes and lizards may be caught, but fewer species of frogs and salamanders. During the first 2 weeks of June, turtles begin to nest.

For a complete assessment of the herpetological community, at least four trapping periods of 3 to 5 days each coinciding with rain in early April, late April–early May, and late May and mid-June are recommended. The following exceptions apply if the area to be censused is farther than 3 km from water: (1) the June trapping period is not necessary because turtles seldom go that far in search of a nesting site; and (2) the early April trapping and late April–early May periods are not needed because salamanders and frogs seldom move more than 3 km between breeding sites and summer home ranges.

Weather

Drift fences may be put in at any time, but traps should be kept closed until rain is expected. The most productive trapping period for amphibians is in the 24 h after a rain starts. They will be active on the surface while temperatures are greater than 4° C.

In Wisconsin, snakes and lizards become active after rains when air temperatures reach 21° C or higher. Overcast humid days above 15° C are ideal for catching aquatic turtles in terrestrial habitats.

Habitat Assessment

This section presents a simplified method for evaluating the habitat characteristics in the sample area and the types of reptiles and amphibians that might be present. This evaluation is necessary for proper trap selection and placement. The analysis is specific to the northern midwestern states, but it can be modified for any site.

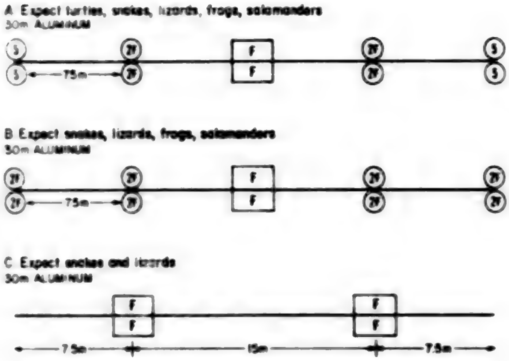
A Expect turtles, snakes, lizards, frogs, salamanders
30m ALUMINUM
S
2F
F
F
2F
S
S
2F
2F
S
7.5m
B Expect snakes, lizards, frogs, salamanders
30m ALUMINUM
2F
2F
F
F
2F
2F
2F
2F
2F
2F
7.5m
C Expect snakes and lizards
30m ALUMINUM
F
F
F
F
7.5m
15m
7.5m

Fig. 17. Type and placement of traps dictated by expectation of catch based on habitat assessment. The symbols 5, 2F, and F refer to the positions of 18.9-L pit traps, 7.6-L pit traps with funnels, and funnel traps.

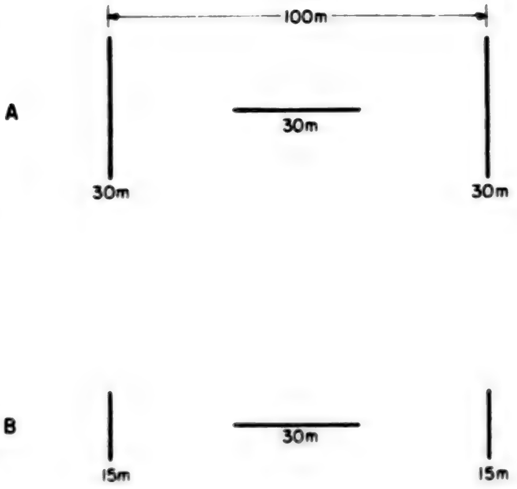

Fig. 18. Proposed placement of drift fences.

If an area is within 3 km of permanent water, expect all major groups of reptiles and amphibians (Fig. 17A). If the area is farther than 3 km from permanent water but within 3 km of temporary ponds, marshes, or streams, or if the area is heavily wooded, expect snakes, lizards, frogs, and salamanders (Fig. 17B). If a prairie, old field, or savannah is more than 3 km from any open water, either permanent or temporary, expect only snakes and lizards (Fig. 17C).

Position and Length of Fence Line

At least two 30-m lengths of fence with traps should be placed 100 m apart parallel to the vegetation gradient and another 30 m set perpendicular to and halfway between the other two lines (Fig. 18A). If two adjoining habitat types are being assessed, a 30-m fence parallel to the habitat gradient and another 30-m fence perpendicular to the gradient is needed in each area to show the difference between use of an area as a home range and use of an area as a migratory corridor. In situations where the width of the habitat does not allow 30-m lengths of fence to be used, 15-m lengths on either side of the line parallel to the strip can be used (Fig. 18B). Areas which are less than 15 m wide need not have any perpendicular fences.

Installation

It is recommended that V-shaped trenches for the fence lines be about 10 cm deep and about 15 cm wide. A wedge of earth can be removed and then replaced firmly in the trench. One side of the trench should be vertical for a tight fit with the fence. The aluminum can be easily cut and bent to go around logs, rocks, or tree roots (Fig. 3). Mounds of soil and rocks can then be placed over those sections to hold them firmly in place. If more than one roll of aluminum is used, they can be joined together by a strip of duct tape on each side after overlapping the aluminum 6-8 cm.

If weather conditions are right for immediate trapping, 2.5 cm of water should be placed in each pit trap. The water prevents dehydration and also kills ants, beetles, shrews, and mice which might otherwise kill or injure other small animals. Holes drilled 2.5 cm up on the sides of the can allow overflow. Digging the pit slightly deeper in the center leaves a cavity for excess water to drain, preventing rain from filling cans and allowing escapes. A wet piece of cloth should be placed in funnel traps to prevent desiccation of the specimens.

Operation

Traplines should be open continuously for the 3- to 5-day trapping period and checked at least every other day. They should be checked within 24 h after heavy rains because of the likelihood of increased animal movement as well as the accumulation of water in the traps. Animals should be removed, identified, and, if necessary, measured, tallied, marked, and released 2 or 3 m away on the opposite side of the fence.

Acknowledgments

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R. Burton made the illustrations. N. J. Scott, Jr., R. Robino, and R. Bruce Bury are greatly appreciated for their numerous editorial comments.

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Appendix

Common and scientific names of reptiles and amphibians cited in text or taken during study in southern Wisconsin.

REPTILES

Turtles

Snapping turtle	*Chelydra serpentina*
Blanding's turtle	*Emydoidea blandingi*
Ornate box turtle	*Terrapene ornata*
Painted turtle	*Chrysemys picta*
Map turtle	*Graptemys geographica*
Spiny soft-shell turtle	*Trionyx spiniferus*

Lizards

Glass lizard	*Ophisaurus attenuatus*
Six-lined racerunner	*Cnemidophorus sexlineatus*

Snakes

Hognose snake	*Heterodon platyrhinos*
Smooth green snake	*Opheodrys vernalis*
Blue racer	*Coluber constrictor*
Black rat snake	*Elaphe obsoleta*
Fox snake	*E. vulpina*
Bull snake	*Pituophis melanoleucus*
Milk snake	*Lampropeltis triangulum*
Prairie garter snake	*Thamnophis radix*
Eastern garter snake	*T. sirtalis*
Brown snake	*Storeria dekayi*
Red-bellied snake	*S. occipitomaculata*

AMPHIBIANS

Caudates

Blue-spotted salamander	*Ambystoma laterale*
Spotted salamander	*A. maculatum*
Tiger salamander	*A. tigrinum*
Central newt	*Notophthalmus viridescens*
Red-backed salamander	*Plethodon cinereus*

Anurans

American toad	*Bufo americanus*
Cricket frog	*Acris crepitans*
Western chorus frog	*Pseudacris triseriata*
Northern gray tree frog	*Hyla versicolor*
Cope's gray tree frog	*H. chrysoscelis*
Spring peeper	*H. crucifer*
Bull frog	*Rana catesbeiana*
Green frog	*R. clamitans*
Leopard frog	*R. pipiens*
Wood frog	*R. sylvatica*

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SUMMARY OF HERPETOLOGICAL COMMUNITY STUDIES

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A Chronological Bibliography, the History and Status of Studies of Herpetological Communities, and Suggestions for Future Research

by

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Abstract

The Chronological Bibliography of Herpetological Community Studies is used to prepare an historic resumé of the field. The taxonomic and geographic distributions of the studies are described, and the contributions of studies of special themes and habitats are identified. Community studies are derived from classical natural history investigations with input from many other disciplines. The clearest recent trend is the sophisticated mathematical analysis of community structure exemplified by the works of Pianka, Inger, and Schoener. Energy flow studies have begun to appear, and the inevitable controversies have sprung up. Another recent development is the large amount of pertinent research being sponsored by a multitude of governmental agencies. The symposium contributions summarized reflect the current state of the art of herpetological community studies. Suggestions for the future include the need for a rigorous examination of our operating assumptions, such as the role of competition, the amount and availability of the resource bases, and the ecological reality of arbitrary communities. The role of sociality needs to be examined in a community context. New field and analytical techniques need to be developed, and long-term studies should receive high priority. Herpetologists working on government projects should take the responsibility for publishing their findings in scientific journals. Detailed prior planning is seen as the most important factor in determining the success of a herpetological community study.

Though research on herpetological communities has expanded greatly in recent years, it still claims only a small proportion of the herpetological literature. For instance, 246 herpetological titles were published in the 1978 volumes of *Copeia*, *Ecology*, *Herpetologica*, and the *Journal of Herpetology*. Of these, only eight (3%) were sufficiently community oriented to include in the Chronological Bibliography of Herpetological Community Studies following this paper. Since all noncaptive reptiles and amphibians live in communities where they interact with other organisms, the opportunities for community research are virtually limitless. This paper is intended to analyze past community studies, to determine their strengths and weaknesses, and to make suggestions for the future that will encourage further research into an area rich in investigative opportunities.

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[1] Deceased: Died at Gainesville, Florida, on 10 December 1981.

In order to see where we are going, it is instructive to see where we have been. Accordingly, the first part of this paper reviews the historical development of herpetological community studies and defines the major driving forces and trends within the field. The raw data for this review are the contents of the bibliography. After the historical summary, the current status of herpetological community studies is defined based on a resumé of the papers in this volume and the current literature. Finally, the perceived trends in these studies are defined, and recommendations are made in which progress can be made in the most productive directions.

The Chronological Bibliography of Herpetological Community Studies was compiled by following the community criteria laid down in the Preface; that is, the studies that are listed involve three or more reptile or amphibian species living in the same area. There should also be enough ecological or behavioral information to enable species comparisons, and their interactions (or lack thereof) may be deduced. The rather extensive literature on mimicry was omitted, largely because most of the material is still very theoretical and speculative, and field tests are lacking. We have not seen all of the studies listed in the bibliography, and several citations were included on the basis of information provided by other authors. We have tried to make the bibliography as complete as possible, but new references are continually coming to our attention. Foreign studies are particularly likely to have been overlooked. It is complete enough, however, to provide an accurate basis for the historical resumé.

History of Studies of Herpetological Communities

Historical Resumé

The origins of studies of herpetological communities are not very remote, although their roots are deeply buried in the explorations of the early collectors and naturalists. Nothing published in the 19th century was community oriented, and interest in the ecological relationships of sympatric reptiles and amphibians grew slowly in the early 1900's. The development of the study of herpetological communities parallels that of the study of ecology itself, with perhaps a 10- to 15-year lag in most subject areas.

As befitting an infant discipline, early studies were descriptive. Picado's (1913) description of Costa Rican bromeliad faunas included reptiles and amphibians, and his holistic approach could well be emulated by present and future workers. Wright's *Life Histories of the Anura of Ithaca* (1914) was an early example of what could be done by an astute observer collecting data at one site over a period of years, and this type of detailed description of the long-term average phenology of the frog fauna has been rarely duplicated for other areas. During the 1920's, similar studies appeared; interestingly enough, all dealt with snakes: Klauber (1924) in southern California, Brimley (1925) in North Carolina, and Loveridge (1927) in Massachusetts. These studies were mainly concerned with documenting activity and, to some extent, habitat preferences.

The same themes were present in the 1930's. Conant (1938) wrote of reptilian activity patterns in Ohio, and Klauber (1939) contributed a study on snakes. Habitat preferences began to be emphasized: Mosauer (1935) described the fauna and its adaptations in a sand dune area, Humphrey (1936) documented altitudinal distributions of Arizona rattlesnakes, and Dunn (1937) produced a paper amplifying Picado's (1913) original observations on bromeliad herpetofaunas. During this same decade, the work of Uhler et al. (1939) on snake food habits foreshadowed the proliferation of similar studies so important in modern community analyses.

The 1940's saw the emergence of the modern type of descriptive study that integrates most of the important aspects of the biology of the organisms – their demography, abundance, habitat preferences, food habits, activity patterns, and enemies. Fitch (1949), who continues to be one of the most active researchers in the field (this volume), produced an excellent integrated study on California snakes, and Hairston's (1949) report on the ecology of Appalachian salamanders is another fine example. An important development during this period was the initial attempts to quantify animal abundances and other important ecological variables. Quantitative descriptions of populations, their food habits, and their habitat preferences are the raw materials for modern community analyses.

The next decade and a half (1950–65) was

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Table 1. *Number of papers dealing with each taxonomic and geographic segment of the herpetofaunal community*. Some papers fit into more than one category and may be tabulated several times.

Region and taxon	Africa	Asia[a]	Australia	Central America[b]	South America	Europe	Totals
Tropics							
Reptiles and amphibians	10	8	1	16	6		41
Lizards	7	2	1	35[c]	1		46
Snakes	6	2	8	2	2		20
Turtles					3		3
Crocodilians					4		4
Frogs	6	6		8	5		25
Salamanders				1			1
Totals	29	18	10	62	21		
Temperate Zone							
Reptiles and amphibians			2	19	2	1	24
Lizards	12		9	40	5	1	67
Snakes	4		2	43			49
Turtles				2			2
Frogs	3	1	2	20	1		27
Salamanders				13			13
Totals	19	1	15	137	8	2	

[a] Includes the East Indies.

[b] Includes the West Indies.

[c] Includes 27 studies restricted to the genus *Anolis*.

largely a period of consolidation and amplification of the trends already established. Habitat preferences continued to be a favorite topic; guts (mostly snake) were analyzed, and other biological characteristics of sympatric species were examined. Increasingly more emphasis was placed on species interactions, and competitive exclusion became a key phrase and focus of analysis (Hairston 1951; Fouquette 1954; Milstead 1957*a*, 1957*b*, 1957*c*, 1965; Pianka 1965). As in other areas of ecology at the time, competition was assumed to be an organizing force in reptile and amphibian communities; however, no one tested the assumption.

In the mid-1960's, community studies had matured to the point where comparisons between communities were being made. The early studies of Brown and Alcala (1961) in the Philippines, Heatwole and Sexton (1966) in Panamá, and Pianka (1965) in the North American deserts are the first models of a field that has burgeoned in the last 10 years. Pianka has continued to be highly productive both in theoretical community comparisons and in natural history studies. At the same time, Barbault (1967) began detailed community studies that would ultimately provide the greatest wealth of quantitative information on entire herpetological communities available today.

Taxonomic and Geographic Distribution of Studies

A tabulation of the taxonomic distribution of the studies in the bibliography (Table 1) reveals that there have been only a few on crocodilians and turtles. The former group is never very speciose in any one area, and crocodilian "communities" are scarce; however, it is surprising that turtles have not received more attention. They are abundant and easily caught in many places, and multispecies aggregations are common. Lizards are often common, diurnal, and conspicuous, and they have been the subject of the majority of studies in both temperate and tropical habitats. Twenty-seven of the total of 33 tropical lizard studies have been carried out on the genus *Anolis* in the West Indies.

Our list of the geographic distribution of the studies in the bibliography is probably biased toward studies in Australia, Africa, and the New World; even so, relatively few community studies have been done in Asia and Europe. The great majority of temperate zone work has been done in North America, and a large proportion of the tropical studies have been done in Central America, including the West Indies. The efforts of a few very prolific workers are largely responsible for several of the totals: Barbault in tropical Africa, Inger in tropical Asia, Schoener in West Antillean *Anolis*, and Pianka in temperate Africa and in Australia.

Special Study Themes

Several ecological and taxonomic systems have received a disproportionate share of attention. The system represented by the genus *Anolis* in the West Indies mentioned above is one of the best examples. Under the guidance of Ernest Williams at Harvard University, many outstanding theoreticians, systematists, ecologists, and behaviorists have developed an impressive body of data and theory that will provide material for integrative studies of evolution and ecology for many years to come.

Other taxonomically-based systems that have been exploited are the North American natricine snakes (Fitch 1941; Hebrard 1951; Carpenter 1952; Fouquette 1954; Fleharty 1967; Burghardt 1968; Hebrard and Mushinsky 1976, 1978; Mushinsky and Hebrard 1977*a*, 1977*b*; Kofron 1978), whiptail lizards (*Cnemidophorus* and *Ameiva*; Milstead 1957*a*, 1957*b*, 1957*c*, 1965, 1972, 1977; Medica 1967; Asplund 1968*b*; Hillman 1969; Schall 1973, 1977; Scudday and Dixon 1973; Scudday 1977; Mitchell 1979; Cuellar 1979), sea snakes (Shuntov 1971; Voris 1974; Dunson 1975; Heatwole 1975*a*, 1975*b*; Limpus 1975; McCosker 1975; Minton and Heatwole 1975; Dunson and Minton 1978; Redfield et al. 1978) and rattlesnakes (Humphrey 1936; Damman 1961; Pough 1966; Klauber 1972). All of these groups, except the rattlesnakes, are largely diurnal forms that are often abundant and have enough species in a genus so that several similar forms may occur in a given spot.

Other faunas that have contributed the raw materials for a large number of papers are desert reptiles (54 papers) and calling and successional studies of frog ponds (21 papers). Again, the attractive combination seems to be an abundance of animals in a habitat where they are easily observed and collected.

Food habits studies are basic to the understanding of any animal community. The bibliography includes 19 titles which are primarily descriptions of the food habits of coexisting species. Almost half of these are studies of snakes, whereas most of the other studies are divided between lizards and amphibians.

Special Habitats

Several specific kinds of habitat have been singled out for special study. The common thread drawing these studies together is that they deal with habitats that either concentrate animals or that have naturally high populations. For instance, bromeliads concentrate both amphibians and reptiles, especially in the dry season (Picado 1913; Dunn 1937; Smith 1941; Neill 1951), and their faunas are rather easily characterized. Similarly, Funderburg and Lee (1968) and Lee (1968, 1969) investigated the herpetological associates of Floridian pocket gophers (*Geomys*), other mammals, and cabbage palms.

Islands have been a favorite laboratory for evolutionary studies since Darwin and Wallace, and they are beginning to be recognized as good places to study community interactions. An attractive feature of most archipelagos is that similar biotic communities tend to be repeated under a similar climate, but the biogeographic history of each island produces a distinct combination of species. Thus, each island can be viewed as a separate evolutionary "experiment." The *Anolis* students mentioned above have exploited the insular features of their fauna to such a degree that there are few comparable mainland studies. Other workers who have successfully used island systems are Soulé (1966), Case (1975, 1978); Dunham et al. (1978); Case et al. (1979); and Bennett and Gorman (1979).

In the early 1950's, a noteworthy subset of herpetological communities spawned a diverse literature. Anchored by Woodbury and his students in Utah, studies of hibernating aggregations of reptiles (most often snakes) became

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popular. The Utah dens have produced several of the few long-term community studies, and the availability of large numbers of research animals has provided opportunities for detailed insight into the biology of the snakes involved. The paper by Brown and Parker in this volume is the latest in these studies, and its conclusions hold little promise for the future of this important study system that has produced so many articles (Woodbury and Hansen 1950; Woodbury 1951; Woodbury and Parker 1956; Hirth 1966; Hirth and King 1968; King 1968; Hirth et al. 1969; Parker and Brown 1973). Other workers that have studied hibernating aggregations of reptiles and amphibians are Neill (1948), Carpenter (1953), Storm (1955), Cooper (1956), and Drda (1968).

Natural History Studies

Modern community studies, even highly theoretical works, have evolved from origins in classical descriptive natural history. Whereas early workers were content to describe communities, many recent studies probe the questions of "how" communities function and "why" communities are structured as they are. Quantitative instead of just qualitative approaches are becoming more common, and new field and analytical techniques are constantly being developed.

Probably the best known herpetological community is that of the University of Kansas Natural History Reservation. For more than 30 years, Henry Fitch and his students have studied the herpetofauna of this tract of land. Much of the information was published as a series of autecological monographs, but recently the data are being analyzed for community patterns (Henderson 1974; Fitch, this volume). There still remains a wealth of information for further integration.

Natural history studies make up the bulk of the bibliography, and the list of recent contributors is long. Outstanding individual records include Rand (1961, 1962, 1964, 1967; Rand and Humphrey 1968; Myers and Rand 1969; Rand and Williams 1969); Heyer (1967, 1973, 1974, 1976*a*, 1976*b*; Dixon and Heyer 1968; Heyer and Bellin 1973); Heatwole and Sexton (Sexton et al. 1964; Heatwole 1966, 1975*a*, 1975*b*, 1976; Heatwole and Sexton 1966; Test et al. 1966; Sexton and Heatwole 1968; Minton and Heatwole 1975); Duellman (1960, 1965, 1967, 1978); Dixon (Dixon and Medica 1966; Dixon and Heyer 1968; Scudday and Dixon 1973; Dixon and Soini 1975, 1977; Staton and Dixon 1977; Henderson et al. 1978, 1979); Milstead (Milstead et al. 1950; Milstead 1953, 1957*b*, 1960, 1965, 1972; Milstead and Tinkle 1969); and Hebrard and Mushinsky (Hebrard and Mushinsky 1976, 1978; Mushinsky and Hebrard 1977*a*, 1977*b*).

The most productive group in the quantitative exploration of herpetological communities has been Robert Barbault and his collaborators, Claude Grenot and Roland Vernet, of the Laboratoire de Zoologie of the Ecole Normale Superieure in Paris. Publishing since 1967, Barbault has authored or coauthored more titles (19) in the bibliography than any other author. Starting in Africa, he quantified the populations, biomass, habitat use, activity cycles, and trophic structure of the reptile and amphibian communities of the Ivory Coast savannahs (Barbault 1967, 1970, 1971, 1972, 1973, 1974*a*, 1974*b*, 1974*c*, 1974*d*, 1975*a*, 1975*b*, 1976*a*, 1976*b*, 1976*c*, 1976*d*). Transferring his experience to Mexico, he continued the same types of studies in Chihuahua (Barbault 1977; Barbault and Grenot 1977; Grenot et al. 1978; Barbault et al. 1978). Grenot and Vernet also investigated North African herpetofaunas (Grenot and Vernet 1972*a*, 1972*b*; Vernet and Grenot 1972*a*, 1972*b*). In recent publications, Barbault and Grenot processed their data using niche overlap theory, and their analyses tend to converge on those of Pianka (Grenot et al. 1978; Barbault et al. 1978). This wealth of material is little known in North America and has not been incorporated into recent reviews (Pianka 1977; Schoener 1977).

Three recent authors have made outstanding contributions by cataloging and analyzing some of the most complex herpetological communities known. Dixon and Soini (1975, 1977) and Duellman (1978) worked intensively for many years on the Amazonian slopes of Peru and Ecuador. Both sets of studies stem from similar sorts of backgrounds: strong systematic training and experience, blended with a natural history approach to the interpretation of communities. These works should provide copious raw material for developing hypotheses on the structure and function of tropical communities.

Other Disciplines

Many other herpetological disciplines such as systematics, physiology, and autecology have contributed to the development of community studies. The debt to alpha taxonomy is obvious but often overlooked. Many ecologists are unaware of the taxonomic problems in their study area and often do not wish to become involved in their solution. At a minimum, every ecological study should deposit properly prepared voucher specimens in a public museum. Neglect of the nuts and bolts of classical taxonomic herpetology can lead to confusion and imprecision in community studies.

Often a wide gulf exists between laboratory physiologists and field ecologists. The few people that have made an attempt to bridge the gap have provided valuable insight into community function that could not be gained in any other way. Clark (1967), Sexton and Heatwole (1968), and Pough et al. (1977) investigated habitat selection and water loss in snake, lizard, and frog communities; Ruibal (1961) and Schall (1977) looked at thermal adaptations in lizards; and Burghardt (1968) studied innate food habits in a water snake community. Fleharty (1967), in the most complete laboratory analysis of a community to date, studied food habits, water loss, specific gravity, and oxygen consumption in garter snakes. The common feature of these studies is that laboratory and field studies were integrated to provide a unique understanding of the communities involved.

Autecological studies have been, and will continue to be, the basis for most of what we know about the ecology of reptiles and amphibians, and there is much in these studies that can be used in community syntheses. However, it is important to remember that a community has properties greater than the sum of the parts, and single species orientations can be misleading in a holistic analysis.

Recent Studies

The greatest number of papers in the "Modern Period," dating from the mid to late 1960's, still deals with "natural history" subjects such as population size and fluctuation, behavior, and food and habitat preferences. These are becoming more and more useful in gauging community interactions for several reasons: past experience has indicated which ecological variables are most likely to yield useful information, comparative studies are much more common, and techniques of studying communities have become more sophisticated. In spite of these developments, the most distinctive trend in recent herpetological literature is the application of theoretical, mathematical approaches to community analysis. These studies will be examined in detail below. Other recent developments in the literature are the studies of energy flows through reptile and amphibian populations, three recent controversies that remain undecided, and the accumulation of a vast body of knowledge buried in government reports.

Theoretical Studies

As studies of herpetological communities became more quantitative in the 1960's, theoretical analyses became possible. Species and the communities they formed were viewed as active agents in dynamic evolutionary systems. Words like "competition" and the "niche" became common, and differential equations proliferated. The concept of strategies, such as reproductive or feeding strategy, was developed, and resource partitioning analyses were extended beyond mere food habits studies. Space, structural features of the habitat, and the time of day or year were also seen as vital resources.

The earliest papers with significant theoretical analyses include Hairston (1951) on Appalachian salamanders, Fouquette (1954) using garter snake food habits, Milstead's series (1957*a*, 1957*b*, 1957*c*) on Trans-Pecos whiptails, and Collette (1961) analyzing the correlation between *Anolis* ecology and morphology. Since then, theoretical considerations have been a large part of many papers, and the development of techniques of analysis have been a major effort for many authors. Three of these workers stand out, both because of their prolific output and the ingenuity, depth, and novelty of their community analyses.

Eric Pianka (1965, 1966), borrowing techniques from the avian community studies of Robert MacArthur, was a leader in applying quantitative techniques to the testing of hypotheses of community structure. He has continued to develop and refine his analyses, and his comparative approach, using widely dispersed diurnal desert lizard systems, has contributed to the robust nature of his conclusions (Pianka 1969*a*, 1971, 1973, 1975; Pianka et al. 1979). Pianka's emphases have been on the detection of the effects of interspecific interactions, primarily competition, on structure within communities, and the elucidation of geographic patterns of lizard diversity. His approach has been fruitful and, as a result, more is known about ecological characteristics of diurnal desert lizard communities than for any other group of reptiles or amphibians (Pianka 1975, 1977). Although concerns for the structural dynamics of entire lizard communities has dominated his work, Pianka has not neglected the natural history of small segments of communities or even single species (Pianka 1969*b*; Pianka and Pianka 1976; Huey and Pianka 1977; Pianka and Huey 1978; and several other papers outside of the scope of this bibliography). Without this solid natural history base, Pianka's more esoteric theoretical conclusions would be much less acceptable to the general herpetological scientific community.

During the same period, Tom Schoener was adapting a system for measuring structural habitat developed by Rand (1964) to quantify niche characteristics in communities of West Indian *Anolis*. Schoener's earliest studies dealt with single species interactions, but he soon used the same techniques to describe patterns and consequences of resource use by multispecies communities. Patterns analyzed have included animal size relations (Schoener 1969, 1970*b*) and food and habitat use (Schoener 1968, 1970*a*, 1974*a*, 1974*b*, 1975; Schoener and Gorman 1968; Schoener and Schoener 1971*a*, 1971*b*).

Robert Inger and his collaborators have applied innovative analytical techniques to large bodies of community data from the Asian tropics and subtropics (Lloyd et al. 1968; Inger and Colwell 1977; Inger 1980). The questions he deals with (habitat use, species packing) are similar to those studied by Pianka, but the approaches are rather different. Much of the difference derives from problems of scale: Pianka treated 4 to 29 sympatric lizard species in his studies, but Inger treated more than 100 species of reptiles and amphibians. Inger has also contributed to our knowledge of the ways that small segments of faunas interact (Inger and Greenberg 1966*a*, 1966*b*; Inger 1969), and Inger and Greenberg (1966*a*) conducted one of the few field experiments on amphibians.

In addition to the prolific workers cited above, a number of other herpetologists have contributed creative analyses to the further development of our theoretical body of knowledge. They are too numerous to list here, but a few deserve mention for the amount and quality of their work: Crump (1971, 1974, this volume), Wilbur (1972; Wilbur and Collins 1973), Heyer (1973, 1974, 1976*b*; Heyer and Berven 1973), Hurtubia (1973; Hurtubia and di Castri 1973), Fuentes (1976), Moermond (1974, 1979), Huey (Huey and Webster 1976; Huey and Pianka 1977; Pianka and Huey 1978; Huey 1979; Pianka et al. 1979), and Case (1975, 1978; Case et al. 1979).

Energy Flow Studies

Strangely enough, herpetological communities have largely escaped the analyses based on energy flows to which other vertebrates were subjected during the era of the International Biological Program when funding for system-oriented ecological research was most easily obtained. Perhaps the thought was that, even at high densities, reptile and amphibian metabolism was so low compared with mammals and birds that their role in community energetics was negligible. Two recent studies indicate that this generality is probably untenable. Burton and Likens (1975*a*, 1975*b*) showed that salamanders in a New Hampshire forest constitute as much of the animal biomass as any other group of vertebrates, and that energy flow through the salamanders is about 20% of that through the birds in the same ecosystem. Bennett and Gorman (1979), working on the arid West Indian island of Bonaire, concluded that lizards were major consumers, and their daily energy requirements exceeded those of small mammal faunas in temperate zone systems. Clearly the assumption that reptiles and amphibians can safely be ignored in analyses of ecosystem energetics needs reexamination, especially in tropical systems.

Controversy

Any field of human endeavor ultimately generates controversy, but the study of herpetological communities seems to be, with few exceptions, relatively free from disagreement. This situation is partly good in that it has allowed a free and objective interchange of ideas without the barriers that are artificially erected when differences of opinion become polarized. On the other hand, we believe that the theoretical underpinnings of much of our work has not been adequately examined, and many operating assumptions are accepted without sufficient review. We will return to this idea in the section on suggestions for the future. There are three theoretical areas with opposing views in the papers of the bibliography. One has very little associated data, and the other two have data that are interpreted in two different ways.

The first is the explanation by Janzen (1976) for an apparent lack of reptiles in Africa when compared with tropical America. Using sweeping correlations, Janzen concluded that the community of scavengers supported by the grazing herbivores in Africa also suppressed the reptile populations. Kreulen (1979) took issue and responded with other correlative observations. Janzen's (1979) reply contained no new information but suggested some tests for his hypothesis.

The second controversy has developed over explanations of the sizes of individuals of the lizard genus *Uta* on islands in the Sea of Cortez. Soule (1966) concluded that the size of utas on islands was determined by the competitive pressure from other iguanid species present. With the collection of more data and further analysis, Dunham et al. (1978) found other variables, such as number of perennial plant species, to be equally well correlated and suggested caution in evaluating correlative data with the *a priori* assumption that competition is the community organizer. The latter authors suggested several ways to remedy the problems that they see in many similar studies.

The third area of controversy lies in differing interpretations of the effects of competition in larval amphibian communities (Heatwole, this volume). Wilbur (1972) and Wilbur and Collins (1973), on the basis of extensive experimentation with *Rana* and *Ambystoma* larvae, concluded that competition was one of the major organizers of many tadpole communities. Heyer (1976*b*) disagreed, and based on his own studies from Thailand, Panama, and the eastern United States, concluded that predation and random factors were usually responsible for observed tadpole community structure, and that interspecific competition was not.

These controversies seem to be rather different, but there is a common thread running through them all: the relative importance of predation and competition as organizers in herpetological communities. Janzen's (1976) hypothesis that predation is a major determinant is based on little data and much speculation, and is obviously intended to be heuristic, but the practical means of testing it are not clear. Soule's (1966) conclusion that *Uta* size depended on competition was tested, and serious doubt was cast on it. Wilbur (1972) and Wilbur and Collins (1973) pinpointed several areas where they believe competition is operating, but Heyer (1976*b*) saw only predation pressure or random effects. At least one side in each of these arguments believes that one of the most powerful tools for generating definitive data is community experimentation (Wilbur and Collins 1973; Tinkle and Gibbons 1977; Janzen 1979).

Governmental Reports

Governments at all levels have suddenly become aware of the presence of a large number of animal species that have been ignored in previous planning. Now land and pesticide use, waste disposal, resource development, and a multitude of other governmental activities require a complete vertebrate inventory or environmental impact statement before the project can be carried out. The preparation of these inventories or statements include the gathering of a great amount of potentially useful information on reptile and amphibian communities. Most of the information is buried in reports with limited distribution which are collectively referred to as "gray literature." We have not attempted to examine this literature here, but we believe it should not be ignored in the future. Part of the problem with using it is in determining its reliability, since it is often not reviewed by competent biologists, and voucher specimens are seldom prepared.

Review of the Symposium

The contents of the symposium largely reflect the current status of research into herpetological communities. Heatwole reviews our current knowledge of community structure to set the stage for the rest of the volume. Crump examines the role of life history strategies as they may affect amphibian communities. Her paper provides several predictions for future research. After the reviews, Wiest describes in detail the anuran succession in a series of Texas ponds, and Jones examines niche relations in West Indian frogs.

Three papers on resource partitioning in snakes follow. The first two are the most recent in a long series of studies on well-known systems. Brown and Parker continue the Utah den series, but recent events appear to indicate that this distinguished series of studies will soon be terminated. Fitch summarizes the food habits of the snakes of the University of Kansas Natural History Reservation. The third paper, by Reynolds and Scott, examines a mammal-eating snake community in Chihuahua, México.

Creusere and Whitford initiate the section on lizard communities. Their paper clearly documents the large amount of individual variation in activity patterns; their work underscores the need to look at individual strategies and not to generalize from observations on total populations. Mautz describes an interesting Mexican cave saurofauna, and Bury provides biomass estimates for a series of Mojave Desert lizard and tortoise faunas.

Scott analyzes an African forest herpetofauna and compares it to previous studies in Asia and Central America.

Three papers describe the attributes of herpetofaunas living on sandy substrates. Werner synthesizes work in the Sinai Desert, Campbell and Christman document faunal succession on sandy sites in Florida, and Smith describes resource partitioning in the most highly adapted sand-swimming segment of the same fauna.

The next three papers describe field techniques for community study that have been proven in extensive studies. Lillywhite used tracking methods to study California snakes, Campbell and Christman used various trapping and collecting methods to gather data on Florida faunas, and Vogt and Hine did the same in Wisconsin.

The mix of papers in the symposium seems to be a fair representation of the current state of herpetofaunal community studies. Many of the subject areas prominent in the historical review are present here: frog pond succession, hypothesis-generating theory, food habits, resource partitioning, special habitats, and mathematical analyses.

Suggestions for the Future

The literature review and the symposium contributions point to several clear recommendations for future work. For instance, the general unavailability and unawareness of Barbault's work in North America underscores the need for much more effective reprint exchange and translation services than we have at present. Recent tendencies to cut back or eliminate foreign language requirements in graduate curricula have certainly contributed to the problem. More personal contacts between workers in different countries would also help.

Another specific area that needs work is the extension of the studies of insular populations of *Anolis* to mainland sites. The West Indian anoles are known in great and voluminous detail, and generalities derived from their study are being extrapolated to many other systems and have threatened to become dogma. However, since these island populations are unusual in many respects, we should be wary of extending the ecological and evolutionary conclusions to mainland forms. From what little that is known, mainland *Anolis* are probably not subject to the same degrees of competitive and predatory pressures as the island ones.

One of the basic assumptions underlying the great majority of resource partitioning studies is that competitive exclusion between species is responsible for the community patterns. Unfortunately, very few attempts have been made to show that competition really exists, and fewer yet have good evidence for its presence. There is a good possibility that competition is an important interaction between island anoles but not between mainland species. Competition is easy to assume and makes a convenient focus for partitioning studies, but we should realize that the best correlations in the world do not prove the importance of competition as a force that structures communities.

One of the few ways to get a better idea of the real importance of competition are experimental studies done in the field. Only two community-level experimental studies have been published so far (Inger and Greenberg 1966*a*; Cuellar 1979), and more work along these lines will be needed before we will be able to say whether our assumption has been correct. In the final analysis, interspecific competition will probably prove to be a major determinant of the structure of some communities, whereas it can be ignored in others.

Another neglected aspect of resource partitioning studies is the determination of resource abundance and availability. Theoretically, for exploitative competition to occur, two species must be using a common, limited resource base. The demonstration of these conditions in a given study would greatly strengthen the assumption of the importance of competition. Perhaps more interaction with quantitatively-oriented entomologists and other biologists will help alleviate the problems of sampling food resources.

Related to the problem of the assumption of competition is the arbitrary nature of herpetological communities. Most workers have not attempted to define their version of the community in ecologically meaningful terms. They have dealt with a convenient subset of the animals present, assuming that the interactions between these species are important in determining structure. Pianka (1973, 1977) is one of the few workers in the area to recognize the potential problems. Detailed study of the relations between herpetological species with no concern for other faunal components of the community could be very misleading. For instance, large spiders, scorpions, and centipedes could conceivably be the most important competitors with forest litter reptiles and amphibians, and an analysis of resource partitioning would be grossly inaccurate without including them. Perhaps a clearer picture would emerge if herpetologists thought in terms of "the reptile and amphibian components of the community" instead of the current usage. Pianka (1973) and Heatwole (this volume) would use the word assemblage in the same context.

Another technique that has been underexploited by researchers is the combined field and laboratory study. The few mentioned above have shed a great deal of light on the adaptations of reptiles and amphibians to their environment, and when a comparative approach is followed, many of the proximate causes for observed community patterns become clear.

Comparing the structure of different communities is a useful technique for detecting global patterns. Pianka has been the leader in developing this method, but the contrasts need not be intercontinental to be useful. Comparisons between a variety of local communities, such as Campbell and Christman's Florida sandhill paper in this volume, can serve to focus attention on faunal patterns that would otherwise be missed. In order to make comparisons between two sites, the data need to be compatible. This is one of the strongest arguments for developing and standardizing techniques that have broad applications in a variety of communities.

The importance of social factors in structuring herpetological communities is almost unknown. Surely the intense territoriality shown by many lizards, frogs, and crocodilians leaves its imprint on the local assemblage. The demographic consequences of high and low population densities have not been investigated. How sensitive are frog choruses, tadpole aggregations, synchronous sea turtle nestings, and other mass activities to low population levels? Most social phenomena in reptiles and amphibians are still poorly known, and their inclusion in an integrated model of community dynamics is a long way in the future.

The development of field techniques for the study of herpetological communities seems to have lagged behind the data gathering in recent years. Papers describing trapping, marking, and census methods were common in the literature of the 1940's and 1950's, but their frequency has dropped in recent years. With field herpetology becoming more and more quantitative, it is necessary to pay more attention to our field methods. Comparisons between techniques are needed, such as Campbell, Christman, Vogt, Hine, and Lillywhite have done in this volume, and methods need to be evaluated over a wide range of habitats. Studies designed for maximum efficiency and utility will then use those methods that give results that can be compared with temperate forest studies because the study techniques have been compatible.

New analytical techniques also need to be developed. Quantitative analyses of community data should be a tool leading to biological understanding and not a goal in itself. If the biological significance of a quantitative procedure is not evident, it should not be used. The checkered history of the information theory parameters, H and H', is a good example. These diversity measurements are useful for quantifying niche features such as food habits or the use of structural features of the habitat. However, when H′ is calculated as a community parameter based on the distribution of individuals among species, its meaning becomes obscure. The community H′ has generated much more heat than light, and correlations with some sort of community "stability" or "maturity" seem to be spurious. To say that one community has a higher H′ than another carries very little information, and what little there is could be better expressed in more intuitive ways.

Long-term studies are much needed. Almost all of our ideas about herpetological communities derive from short-term "snapshots" of the system. Reptile and amphibian populations vary considerably from year to year; relative species densities fluctuate and some species disappear to be replaced by others. Clearly, conclusions based on one instant in this dynamic system are bound to be misleading. Long-term studies are not easily supported and are often neither cost nor time efficient if volume of publications is the currency of the trade. However, if we are ever going to be able to say with confidence that we understand the functioning of a herpetological community, it will have to be after the community has been studied for many years.

Future studies will inevitably be more concerned with the effects of humans on herpetological communities. There have been a few studies in the past that have dealt with subjects such as urban herpetofaunas, and we foresee a proliferation of these in the future. As humans have an ever greater impact on the environment, we will want to focus on such questions as the community impacts of pesticides and the effects of habitat simplification. Another subject of increasing concern is the evaluation of the results of "island" size on diverse herpetological communities now that it is clear that in the near future there will be no longer any large blocks of continuous natural habitat in many parts of the world.

Herpetologists funded by governmental agencies should shoulder greater responsibilities, taking great pains to see that the data are accurately gathered and that the realities of funding and deadlines are not allowed to compromise the quality of the data and the report. Funding agencies should be made aware of the levels of money and time necessary to do a proper job. If enough funds are not available, a more limited study should be designed. A major characteristic of many governmental surveys is the attempt to cover vast areas of geography, numbers of taxa, and kinds of habitats by using superficial techniques designed only to satisfy a bureaucratic end. A professional herpetologist trapped into this kind of situation is not likely to derive satisfaction from the results. A second responsibility of those directing governmentally funded studies is to see that the results are published in a reviewed journal. As mentioned above, the huge volume of gray literature embodied by in-house reports is almost unusable. If the data are worth gathering, they are worth reporting. A third obligation of any biologist, but especially those working on governmental projects, is to deposit adequate series of voucher specimens in an established public museum. This serves to protect both the worker and the government. Government contract officers need to be educated to this necessity and should be prepared to pay their fair share of the costs of specimen preparation and curation. Unfortunately, most agencies are still parasitizing the museums they use, although many curators now have established charges for their services.

Many other recommendations could be made concerning how to increase the effectiveness of community studies, but perhaps the most important one refers to study design. The most sophisticated studies are those that are well planned from the beginning. Pianka, Schoener, and Inger knew what they wanted to measure before they went into the field, and they had a fairly good idea of what questions they were trying to answer. When it came time to analyze the data, they had the necessary measurements. Before a field person devotes a substantial amount of time and other resources to a study, they should as clearly as possible outline the questions they wish to ask and the data they need to answer them. In this way, many descriptive studies could be turned into much more useful examinations of community structure and function.

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